DISTRIBUTIONS AND INTERACTIONS OF CO-OCCURRING ESTUARINE FOUNDATION SPECIES

SEAGRASSES, SEAWEEDS, AND SHELL-FORMING ORGANISMS

A thesis submitted in partial fulfilment of the requirements for the Degree of Doctor of Philosophy, in the School of Biological Sciences at the University of Canterbury, New Zealand

Travis Hauri Foster

2019

UC UNIVERSITY OF CANTERBURY
Te Whare Wānanga o Waitaha
CHRISTCHURCH NEW ZEALAND

MARSDEN FUND
TE PŪTEA RANGAHAU A MARSDEN

ROYAL SOCIETY TE APĀRANGI

ABSTRACT

Many ecosystems and habitats around the world, such as mangroves, forests and sedimentary estuaries, are dominated by relatively few species with widespread effects on biotic and abiotic functions. These critical organisms are known as foundation species; they define the structure of a community by creating habitats, competitive dominance, regulating ecosystem dynamics, and/or acting as a disturbance agent. Multiple foundation species often co-occur within these systems; for example, when mistletoes are attached to trees in forests, or seaweeds are found entangled around seagrasses. These co-occurring foundation species can potentially lead to facilitative (such as habitat cascades, plant-pollinator interactions, or nursery functions) or negative (competition, predation/herbivory, or parasitism) interactions. While negative interactions have been meticulously studied, a research gap exists about facilitative interactions between foundation species, and if these interactions are fixed, or change, through space and time. The main objective of this thesis is to determine co-occurrence patterns of estuarine foundation species, quantify their interactions, and their impact on estuarine communities, along temporal, spatial, and stress gradients. I addressed this objective by (i) reviewing and analysing published experiments testing for interactions between common estuarine foundation species, (ii) quantifying, through surveys, co-occurrence patterns of estuarine foundation species along spatio-temporal gradients in New Zealand, (iii) quantifying, through experiments, interactions between foundation species and how these interactions may change from negative to positive depending on densities, disturbances and scales, and (iv) identifying overlooked foundation species in New Zealand estuaries.

In Chapter 1 I introduce the model organisms and study areas I use throughout this thesis. These organisms act as foundation species in different ways, and physiologically differ, but all are important to their communities. The seagrass *Zostera marina* is a perennial fixture in many estuaries and can create large beds leading to high biodiversity compared to surrounding sediments. The seaweeds *Gracilaria chilensis* and *Ulva* spp. are more ephemeral, but still provide habitat, food, and stress reduction (when not blooming) to invertebrates. Shell-forming organisms such as the bivalve *Austrovenus stutchburyi* and many snails biogenically produce hard substrate through their shells that many organisms utilize in soft-sediment systems. These shells will persist long after the death of the organism, and can become important foundation species themselves, known as a legacy effect or taphonomic feedback. These foundation species were studied in 15 estuaries around the South Island of

New Zealand from three latitudinal regions from one-time sampling events, with a special emphasis on the Avon-Heathcote Estuary, where many studies and experiments were done over 3 years.

In Chapter 2, I use meta-analysis of 82 publications, to document reciprocal interactions between common marine and freshwater foundation species: macroalgae, angiosperms, and bivalves, as well as identify research gaps about these interactions. I found typical 'ecological publication bias'; most experiments were conducted in temperate climates, in developed countries, and over short durations (only three experiments lasted more than 2 years). Furthermore, experiments between freshwater foundation species (9% of studies) and experiments documenting effects of bivalves on macroalgae (4%) were few in number. In the meta-analysis I found negative effects of macroalgae, positive effects of bivalves, and no net effect of angiosperms, on other aquatic foundation species, and that small foundation species were more negatively affected than larger foundation species. These findings were robust across geographical latitudes, ecosystem type, and experimental durations and conditions, except that the negative effect from macroalgae were more severe in laboratory than field experiments.

In Chapter 3, I quantify co-occurrence patterns between seaweeds and seagrass in 14 estuaries across three latitudinal regions on the South Island of New Zealand and at different seasons and elevation levels in the Avon-Heathcote Estuary, as well as their effects on shell-forming organisms. I found that seagrass and seaweeds co-occurred in all estuaries (25% of all photographs), and annually (62% of photographs). I also found that seaweeds as well as seagrass, had a large positive impact on densities of shell-forming taxa (73% and 32% higher respectively), especially trochid snails, likely consuming the seaweed and inhabiting the seagrass to avoid predation. There was no additional facilitative effect on shell-formers when seagrass and seaweed occurred together in the latitudinal survey, but in the temporal survey when seagrass and seaweed co-occurred, shell-formers densities were 48% higher than on seaweed alone, and 155% higher than seagrass alone. I also found that trochid snails, in seagrass and seaweed samples, were 2.5× more abundant in winter than in summer, even though seagrass and seaweed biomass were higher in summer samples.

Chapter 4 examines in detail how 'habitat-using organisms' co-occur with 'habitat-forming organisms' in the same estuaries that were studied in Chapter 3. Based on close-up field observations, I recorded how estuarine organisms (habitat-users) were associated with

biogenic host-species (habitat-formers). I found that the bivalve *Austrovenus stutchburyi*, the dead shells of *Austrovenus*, and, more surprisingly, trochid snails, were among the most important habitat-formers (being inhabited by most organisms and most species) in New Zealand estuaries, providing biogenic hard-substrate habitats in all the sampled estuaries, elevation levels, and time periods.

Chapter 5 explored how the coexisting and morphologically similar trochid snails *Diloma nigerrimum* and *Micrelenchus huttonii* acted as foundation species from both top-down (grazing pressure) and bottom-up (habitat provision) perspectives. Both snails were commonly distributed in 15 sampled estuaries, although both taxa were not always present in each estuary. In a two-year seasonal survey from the Avon-Heathcote Estuary, the snails were present year-round and throughout habitats and tidal elevations. In a grazing experiment, *Micrelenchus* had stronger top-down effects than *Diloma* in all experiments with higher grazing rates on the coarsely branched red seaweed *Gracilaria* than the thin sheet-forming green seaweed *Ulva* (up to 22× more in the lab and 12× more in the field), whereas seagrass was grazed insignificantly. *Micrelenchus* also provided habitat to 3× more epibionts than *Diloma* and had more epiphytized shells (57% vs 43%), although *Diloma* had more *Ulva* recruits per shell (3.2 ± 0.6 vs 0.9 ± 0.1). This shows that even though the two snails are similar, they fulfil the role of foundation species in distinctive ways.

Chapter 6 hypothesises that bivalve shells can be considered ubiquitous ‘dead but functioning’ estuarine foundation species. This hypothesis was tested by quantifying (i) spatial distributions of empty shells in six estuaries in three regions in New Zealand, (ii) temporal distributions of shells in the Avon Heathcote estuary from 2014 to 2016, and (iii) impacts of shells on benthic communities. I found that dead shells were present in all estuaries (ranging from 0.2% to 30% cover of the sedimentary substrate) and all time periods (ranging from 4.3% to 17.8% cover across seasons). Importantly, invertebrate densities were from two (experimental data) to five (survey data) times higher in shell habitats compared to bare sediments. Finally, I found that dead shells within seagrass beds decreased growth of seagrass by ca. 58% compared to the absence of shells.

Finally, in Chapter 7, I discuss my results in a functional framework related to the ecology and attributes of ‘ephemeral solitary macroalgae’, ‘persistent clonal angiosperms’, and ‘long-term persistent solitary and accumulating shells’. I conclude that these types of foundation species often coexist and interact in estuaries where they provide habitat to a wide range of

habitat-using organisms, and either facilitate or inhibit other aquatic foundation species, depending on densities, sizes and environmental conditions. I also conclude that several often overlooked organisms, such as small snails and bryozoans, can be important aquatic foundation species, and that shell-forming foundation species leave a persistent legacy because dead shells provide ubiquitous hard substratum habitat in sedimentary systems.

ACKNOWLEDGMENTS

What a whirlwind journey it has been these past 4 years! I have met and received help from many amazing people during my time in New Zealand, that has made me a better scientist and person.

First, I would like to thank the University of Canterbury for supporting me for three years via the Doctoral Scholarship, which let me live in New Zealand while conducting my research here. Also, I would like to thank the Marsden Fund for helping to fund field and laboratory supplies during my time at University of Canterbury.

I would also like to thank my advisors Dr. Mads S. Thomsen, and Distinguished Professor David R. Schiel for their scientific advice, financial support when my scholarship ended, letting me follow my ideas and develop my own projects, overall support, and getting this thesis to where it is now. You have helped me become a better ecologist (and scientific writer!) and I learned many unexpected and new tricks of the trade from you both.

Of course, I would not have gotten this far without the support, encouragement, and love of my friends in Office 238 and in Banks Peninsula. Mental health coffees, brownies, and lunches outside! Don't forget to take those breaks and enjoy the sun. You all really were the main support group for me, your friendship means the world to me. I look forward to seeing you all again when we've all succeeded!

TABLE OF CONTENTS

ABSTRACT i
ACKNOWLEDGMENTS v
TABLE OF CONTENTS vi
LIST OF FIGURES xi
LIST OF TABLES xvii

CHAPTER 1 GENERAL INTRODUCTION 1

OVERVIEW OF FOUNDATION SPECIES 1
SEAGRASSES AS FOUNDATION SPECIES 2
SEAWEEDS AS FOUNDATION SPECIES 3
BIVALVES AS FOUNDATION SPECIES 4
MOBILE FOUNDATION SPECIES 5
LEGACY EFFECTS OF FOUNDATION SPECIES 5
INTERACTIONS BETWEEN COEXISTING FOUNDATION SPECIES 6
Seagrass-Seaweed interactions 8
Seagrass-Bivalve interactions 8
Seaweed-Bivalve interactions 10
Seagrass-Seaweed-Bivalve interactions 11
MAIN STUDY AREAS 12
THESIS OUTLINE 13
FIGURES 16
REFERENCES 21

CHAPTER 2 A GLOBAL REVIEW AND META-ANALYSI OF ESSECTS OF CO-OCCURRING MACROALGAE, ANGIOSPERMS, AND BIVALVES 34

ABSTRACT 34
INTRODUCTION 34
Species interactions and foundation species 34
Interactions among aquatic angiosperms, macroalgae, and bivalves 35
Global review and meta-analysis 37
METHODS 38
Data collection 38
Data extraction and effect size calculation 38
Meta-analysis 40
RESULTS 40
Global review 40
Meta-analysis 41

DISCUSSION 42
Global review 42
Meta-analysis 44
CONCLUSIONS 49
FIGURES 50
REFERENCES 54
SUPPLEMENTARY MATERIAL 65
Supporting tables and figures 65
Statistical results 68
List of retained publications 72
CHAPTER 3 DISTRIBUTIONS AND INTERACTIONS AMONG SEAGRASS AND SEAWEED AND ASSOCIATED SHELL-FORMING COMMUNITIES IN NEW ZEALAND ESTUARIES 77
ABSTRACT 77
INTRODUCTION 78
METHODS 80
Study Areas 80
Distribution of seagrasses and seaweeds 81
Effects of seagrass and seaweed on shell-forming invertebrates 82
Field Experiment 1: effects of seagrass, seaweed and mussels 83
Field Experiment 2: effects of seagrass and seaweed 84
RESULTS 85
Distribution of seagrass and seaweed 85
Effects of seagrass and seaweed on shell-forming organisms 86
Field Experiment 1: effects of seagrass, seaweed and mussels 87
Field Experiment 2: effects of seagrass and seaweed 88
DISCUSSION 89
Distributions of estuarine foundation species 89
Effects of seagrass and seaweed on shell-forming bivalves and snails 89
Effects of mussels and seaweed on seagrass 91
Effects of seagrass and mussels on seaweed 92
CONCLUSIONS 92
TABLES 94
FIGURES 105
REFERENCES 117
SUPPLEMENTARY MATERIAL 125

CHAPTER 4 BIOGENIC HABITAT INTERACTIONS IN ESTUARIES: ASSESSMENT OF HABITAT-USERS AND HABITAT-FORMERS IN NEW ZEALAND 127

ABSTRACT 127

INTRODUCTION 128

METHODS 130

Study sites 130

Latitudinal survey 131

Surveys in the Avon Heathcote Estuary 132

RESULTS 133

Latitudinal survey 133

Surveys in the Avon-Heathcote Estuary 135

Quadrat size comparison 136

DISCUSSION 136

Latitudinal and elevation patterns 137

Species and habitat types 138

Night vs. day and quadrat sizes 140

Conclusions 142

TABLES 143

FIGURES 147

REFERENCES 156

SUPPLEMENTARY MATERIAL 166

CHAPTER 5 DEAD SHELLS AS FOUNDATION SPECIES: LEGACY EFFECTS FROM AN ESTUARINE BIVALVE IN NEW ZEALAND 167

ABSTRACT 167

INTRODUCTION 167

METHODS 171

Study sites 171

Distributions of dead shells in estuaries 171

Effects of dead shells on benthic communities 172

RESULTS 174

Distributions of dead shells in estuaries 174

Effects of dead shells on benthic communities 175

DISCUSSION 177

Distributions of dead shells in estuaries 178

Effects of dead shells on benthic communities 178

The value of dead shells 180

Conclusions 181
TABLES 182
FIGURES 188
REFERENCES 197
SUPPLEMENTARY MATERIAL 205

CHAPTER 6 ESTUARINE SNAILS AS MOBILE FOUNDATION SPECIES: DISTRIBUTIONS, GRAZING RATES, AND HABITAT FORMATION 207

ABSTRACT 207
INTRODUCTION 208
METHODS 209
Distribution 209
Top-down grazing effects 211
Bottom-up habitat provision 213
RESULTS 214
Distribution 214
Top-down grazing effects 215
Bottom-up habitat provision 217
DISCUSSION 218
Distribution 218
Top-down grazing 221
Bottom-up habitat provision 222
Conclusions 223
TABLES 225
FIGURES 232
REFERENCES 239

CHAPTER 7 GENERAL DISCUSSION 245

DISTRIBUTIONS OF FOUNDATION SPECIES 245
Latitudinal patterns 245
Seasonal patterns 246
INTERACTIONS AMONG CO-OCCURRING FOUNDATION SPECIES 247
Seagrass and seaweeds 247
Seagrass and shell-formers 247
Seaweed and shell-formers 248
FOUNDATION SPECIES INTERACTIONS WITH BENTHIC COMMUNITIES 249
CONCLUSIONS 250
FIGURES 252

REFERENCES 254

LIST OF FIGURES

Chapter 1

Figure 1.1 Examples of the habitats created by estuarine foundation species in New Zealand: the seagrass *Zostera muelleri* (A, B), the seaweeds *Ulva* spp (C) and *Gracilaria chilensis* (D), and shell-forming organisms like the cockle *Austrovenus stutchburyi* (E), the snail *Micrelenchus huttonii*, (F) and dead shell accumulations (G, H). Photos represent 1 m^2 except for A, E, and F.*Micrelenchus huttonii*, (F) and dead shell accumulations (G, H). Photos represent 1 m^2 except for A, E, and F..... 16

Figure 1.2 Examples of legacy effects of marine seagrass, seaweeds, and bivalves. Graphics used are from Integration and Application Network, University of Maryland Center for Environmental Science, as well as by the author..... 17

Figure 1.3 Examples of positive (green arrows) and negative (red arrows) interactions between (A) seagrass and seaweeds, (B) seagrass and bivalves, and (C) seaweeds and bivalves. Graphics used are from Integration and Application Network, University of Maryland Center for Environmental Science. 18

Figure 1.4 Locations of estuaries sampled in this thesis. (A) 16 estuaries from three latitudinal regions around the South Island of New Zealand, and (B) a detailed view of sampling locations within the Avon-Heathcote Estuary in Christchurch, New Zealand. 19

Figure 1.5 Graphical outline of themes from each data chapter in this thesis. Graphics used are from Integration and Application Network, University of Maryland Center for Environmental Science, as well as by the author. 20

Chapter 2

Figure 2.1 Location of experiments published in 82 scientific papers reporting impacts of angiosperms, macroalgae, or bivalves on each other, and therefore included in this review and meta-analysis..... 50

Figure 2.2 Number of peer-reviewed publications used in this review and meta-analysis classified by (A) climate zones (polar ≥66°, temperate = 65-36°, subtropical = 35-23°, tropical = 22-0°), (B) marine and freshwater systems for different types of interactions (the first organism is the independent and the second is the dependent; Alg = macroalgae, Ang = angiosperms, Biv = bivalves), (C) year of publication and (D) experimental duration. 51

Figure 2.3 Meta-analysis. Hedge's *g* effect sizes ± 95% CI quantifying impacts of angiosperms (Ang), macroalgae (Alg), and bivalves (Biv) (A) on other aquatic foundation species, (B) on small (Sm), medium (Med) and large (Lg) foundation species, (C) in field or laboratory (Lab) experiments and (D) in marine (Mar) or freshwater (FW) systems. Negative values are considered antagonistic interactions, while positive effects are facilitative. The numbers of independent effect sizes used to calculate average effect sizes and confidence intervals are shown in parentheses. 52

Figure 2.4 Meta-analysis. Hedge's *g* effect sizes quantifying impacts of angiosperms, macroalgae, and bivalves moderated by (A) Geographic latitude (absolute value, $g = 0.578 + 0.005 \times$Latitude, p = 0.517, * = 42, 39.21 outlier) and (B) Experimental duration ($g = -0.346 - 0.005 \times$Exp. Length, p = 0.702, * = 0.75, 39.21 outlier)..... 53

Chapter 3

Figure 3.1 Map of sampled estuaries around the South Island of New Zealand, from a latitudinal survey (left, middle), and a temporal survey in the Avon-Heathcote Estuary. 105

Figure 3.2 Percent cover of seagrass vs. seaweed from a latitudinal survey from 15 estuaries on the South Island of New Zealand. There was a significant negative relationship between cover of seagrass and seaweed. White, grey and black symbols represent northern, central estuaries, and southern

estuaries, respectively. 343 (25%) of all samples had co-occurring seagrass and seaweed, 500 (37%) had only seagrass, 316 (23%) only seaweed, and 177 (13%) neither seagrass or seaweed. 106

Figure 3.3 Percent cover (mean ± SE) of seagrass, seaweed, dead shells, bare sediment and rocks in 15 estuaries from three latitudinal regions around the South Island of New Zealand (see Figure 1.1 for names of estuaries). 107

Figure 3.4 Percent cover of seagrass vs. seaweed from a seasonal survey in the Avon-Heathcote Estuary. There was a significant negative relationship between cover of seagrass and seaweed. White and black symbols represent Plover and Tern street samples, respectively. 618 (62%) of all samples had co-occurring seagrass and seaweed, 124 (12%) had only seagrass, 187 (19%) only seaweed, and 64 (6%) neither seagrass or seaweed. 108

Figure 3.5 Percent cover (+ SE) of seagrass, seaweed, dead shells, bare sediment, and rocks at (A) Tern Street and (B) Plover Street, in early/late summer (December-March) and winter (May-August) from 2014 to 2016 in the Avon-Heathcote Estuary (data for August 2015 (both sites) and November 2015 (Plover only) were lost). 109

Figure 3.6 (A) Percent composition of shell-forming taxa (snails, bivalves) from all samples taken from an estuary. (B) Shell-former density (+SE) and (C) taxonomic richness in each sampled habitat treatment from each estuary. Estuary names relate to those in Figure 1. The first 6 estuaries (Pup to Nga) are northern, central estuaries are Rob to AHE, and the last 5 (Dowl to New) are southern. 110

Figure 3.7 Densities (+SE) of shell-forming snails and bivalves from sediment cores in the Avon-Heathcote Estuary pooled across (A) Year (2015 vs 2016), (B) Season (summer vs winter), (C) Site (Plover vs Tern Street), (D) Elevation (subtidal vs intertidal), and (E) Habitat (Seagrass, Seaweed, Seagrass+Seaweed (SG+SW), and Bare sediments). 111

Figure 3.8 Taxonomic richness (+SE) of shell-forming invertebrates snails and bivalves from sediment cores in the Avon-Heathcote Estuary pooled across (A) Year (2015 vs 2016), (B) Season (summer vs winter), (C) Site (Plover vs Tern Street), (D) Elevation (subtidal vs intertidal), and (E) Habitat (Seagrass, Seaweed, Seagrass+Seaweed (SG+SW), and Bare sediments). 112

Figure 3.9 Experiment 1. Density (A, C, E) and taxonomic richness (B, D, F) (+SE) of shell-forming snails and bivalves grouped into three levels of seagrass (A, B), mussels (C, D), and *Ulva*-seaweed (E, F) in the Avon-Heathcote Estuary. Samples (n = 36) were collected with a sediment corer (9 cm diameter × 10 cm depth). Removed = seagrass removed by cutting leaves at the sediment surface, Cut = seagrass leaves cut to half their length, Control = undisturbed seagrass control. '+' = the number of mussels added to each plot. 'mL' = volume of wet *Ulva* added to each plot. 113

Figure 3.10 Experiment 1. Seagrass root biomass (+SE, grams dry weight) for different levels of (A) seagrass manipulation (control, cut, removed) and mussel addition (0, 1, 4 mussels, n = 12) and (B) seaweed additions (0 mL, 150 mL, 500 mL, n = 36) in the Avon-Heathcote Estuary. Samples were collected with a sediment corer (9 cm diameter × 10 cm depth). 114

Figure 3.11 Experiment 2. Density (A, C) and taxonomic richness (B, D) (+SE) of shell forming snails and bivalves for different levels of (A, B) seagrass leaves (control, cut, removed, n = 15) and (C, D) *Ulva* seaweed (0, 150, 500 mL wet *Ulva*, n = 9 for 0 mL, n = 18 for others) in the Avon-Heathcote Estuary. 115

Figure 3.12 Experiment 2. Biomass (+SE) of seagrass (A) above ground leaves (evaluted from undisturbed seagrass 'controls', n = 3) and (B) below-ground roots and rhizomes (evaluated across all seagrass treatments, n = 9) in the Avon-Heathcote Estuary for three levels of *Ulva* seaweed (0, 150, 500 mL wet volume). 116

Chapter 4

Figure 4.1 Site locations and names of estuaries sampled on the South Island of New Zealand in a latitudinal survey (left, middle) and various surveys in the Avon-Heathcote estuary (right) of benthic habitat-formers and habitat-users. 147

Figure 4.2 Percent cover (+SE) of benthic habitats types in 14 estuaries grouped into three latitudinal regions at (A) low and (B) high tidal elevation, on the South Island of New Zealand. Quadrat size = 0.010 m^2. 148

Figure 4.3 (A) Number (+SE) of habitat interactions (m^{-2}), (B) richness of habitat-formers and (C) richness of habitat-users in 14 estuaries grouped into three latitudinal regions at low and high elevation, on the South Island of New Zealand. Quadrat size = 0.010 m^2. 149

Figure 4.4 (A, C, E) Percentage of habitat-interactions for individual habitat-formers in 14 estuaries grouped into three latitudinal regions (the sum of all interactions in each region = 100%) on the South Island of New Zealand. (B, D, F) Number (+SE) of habitat interactions for individual habitat-formers (m^{-2}) across latitudinal regions. All data were pooled across two tidal elevation levels. Note scale differences on the y-axes. Quadrat size = 0.010 m^2. 150

Figure 4.5 Percent cover (+SE) of benthic habitats types from sites with different environmental conditions at (A) low and (B) high tidal elevation, in the Avon-Heathcote Estuary. Quadrat size = 0.0625 m^2. 151

Figure 4.6 (A) Number (+SE) of habitat interactions (m^{-2}), (B) richness of habitat-formers and (C) richness of habitat-users from sites with different environmental conditions at low and high elevation, in the Avon-Heathcote Estuary. Quadrat size = 0.0625 m^2. 152

Figure 4.7 (A, C, E, G) Percentage of habitat-interactions for individual habitat-formers across sites with different environmental conditions (the sum of all interactions in each region = 100%) in the Avon Heathcote Estuary. (B, D, F, H) Number (+SE) of habitat interactions for individual habitat-formers (m^{-2}) across sites with different environmental conditions. All data were pooled across two tidal elevation levels. Note scale differences on the y-axes. Quadrat size = 0.0625 m^2. 153

Figure 4.8 (A) Number (+SE) of habitat interactions (m^{-2}), (B) richness of habitat-formers, and (C) richness of habitat-users, of mobile organisms in day or night samples, in a seagrass bed near Plover Street, in the Avon-Heathcote Estuary. Quadrat size = 0.010 m^2. 154

Figure 4.9 (A) Number (+SE) of habitat interactions (m^{-2}), (B, C) richness of habitat-formers, and (D, E) richness of habitat-users, in small (0.010 m^2) and large (0.0625 m^2) quadrats in habitats dominated by mud (Bare), dead shells (Shell) or seagrasses (SG) near Tern Street in the Avon-Heathcote Estuary (n = 3 for each combination of quadrate size and habitat). Associated species-area rarefaction curves of taxa richness for the small and large quadrats are shown in (C) for habitat-formers and (E) for habitat-users. 155

Chapter 5

Figure 5.1 (A) Locations of six estuaries on the South Island of New Zealand sampled in a large scale latitudinal survey and where a shells addition experiment were carried out. **(**B) Locations of sites surveyed in the Avon-Heathcote Estuary from 2013 to 2016. Plover and Tern streets are seagrass dominated sites, whereas the Causeway and Oxidation pond sites are dominated by silty unvegetated sediments. The Heathcote River flows into the estuary in the southwest corner, while the Avon River flows from the northern side. The estuary opens into the Pacific Ocean in the southeast corner. 188

Figure 5.2 Percent cover (+SE) of dead shells, seagrass, seaweed and bare sediments in six estuaries across three latitudinal regions on the South Island, New Zealand. 189

Figure 5.3 Percent cover (+SE) of dead shells, seagrass, seaweed and bare sediments in silty (no seagrass, Oxidation Ponds, Causeway) and seagrass dominated (Plover and Tern Street) habitats in the Avon-Heathcote Estuary in summer 2014. 190

Figure 5.4 Percent cover (+ SE) of dead surface dwelling shells, seagrass, seaweed and bare sediment at (A) Plover Street and (B) Tern Street, in early/late summer (December-March) and winter (May-August) from 2014 to 2016 in the Avon-Heathcote Estuary (data for August 2015 (both sites) and November 2015 (Plover only) were lost). 191

Figure 5.5 Epibenthic invertebrate (A) densities and (B) taxonomic richness (+SE) in summer 2014 from three habitats with and without presence of dead shells (collected from 4 sites in the Avon-Heathcote Estuary). Bare = unvegetated sediments, Shell = dead shells on the sediment, Seagrass = *Zostera muelleri*, and Ulva = the green seaweeds *Ulva* spp., quadrat size = 17 cm × 17 cm (0.0289 m^2), black bars = presence of dead shells. 192

Figure 5.6 Non-metric multidimensional scaling (NMDS) plot of epibenthic invertebrate community structures (samples from summer 2014) associated with three habitats with (black) and without (white) dead shells. Bare = unvegetated sediments, Shell = dead shells on the sediment, Seagrass = *Zostera muelleri*, and Ulva = the green seaweeds *Ulva* spp., quadrat size = 17 cm × 17 cm (0.0289 m^2). 193

Figure 5.7 Invertebrate (A) density (m^{-2}) and (B) taxonomic richness ($core^{-1}$) and recruiting seaweed (C) density (m^{-2}) and (D) richness ($core^{-1}$, = 9 cm circular diameter) recruited onto out-transplanted shells, from an experiment conducted in six estuaries from three regions (North, Central, South) on the South Island of New Zealand. Shell = presence-absence of shells (adding 10-15 shells per plot). Habitat = bare sediments, seagrass habitat with leaves cut (Cut), and undisturbed natural (Nat) seagrass, black = presence of dead shells. Note that seaweed responses were only relevant to test in the shell addition treatment (and therefore excluded the Shell-test factor). 194

Figure 5.8 A non-metric multidimensional scaling (NMDS) plot of benthic invertebrate community structure (samples from summer 2016) from an experiment conducted in six estuaries from three regions (North, Central, South) on the South Island of New Zealand. Shell = presence-absence of shells (adding 10-15 shells per plot). Habitat = bare sediments, seagrass habitat with leaves cut (Cut), and undisturbed natural (Nat) seagrass, black = presence of dead shells. 195

Figure 5.9 Seagrass (A) leaf biomass, (B) root and rhizome biomass, and (C) shell retention, from an experiment conducted in six estuaries from three regions (North, Central, South) on the South Island of New Zealand. +Shell = presence of shells (adding 10-15 shells per plot). Habitat = bare sediments, seagrass habitat with leaves cut (Cut), and undisturbed natural (Nat) seagrass, black = presence of dead shells. Note that seagrass responses were only relevant to test in the seagrass habitat (and therefore excluded the bare mud habitat), whereas the shell retention response only was relevant to test in the shell addition treatment (and therefore excluded the Shell-test factor). 196

Chapter 6

Figure 6.1 (A) Map of 15 sampled estuaries on the South Island of New Zealand divided into a northern (estuary A-F), central (G-H) and southern (J-M) region. (B) Morphology of the two trochid snails *Diloma nigerrimum* and (C) *Micrelenchus huttonii. Diloma* is typically wider than tall in a depressed-globose shell shape, and usually found on sediments and hard substrates in low, mid, and high tide zones (Jones et al. 2005). The maximum height of *Diloma* is 24 mm (Powell 1979). *Micrelenchus* is smaller (maximum height of 15 mm) (Marshall 1998) and the shell is taller than wide in a conico-turbinate shape, and are usually found on seaweed or seagrass in the low to mid tide zones (Jones et al. 2005). Note that drawings are not to scale. 232

Figure 6.2 Densities of *Micrelenchus huttonii* vs. *Diloma nigerrimum* in 15 estuaries on the South Island of New Zealand. There was a weak significant positive relationship between the two snail taxa.

White symbols represent northern estuaries, grey symbols are central estuaries, and black symbols are southern estuaries. There were 221 samples (58% of all collected cores) without any *Micrelenchus* or *Diloma*. 233

Figure 6.3 Mean densities (+SE) of the trochid snails *Diloma nigerrimum* (A, B) and *Micrelenchus huttonii* (C, D) in four habitat types (A, C) and two tidal elevations (B, D) from 15 estuaries around the South Island of New Zealand. Samples were collected by benthic cylindrical cores, 9 cm diameter × 10 cm depth. Dashed lines show estuaries classified by latitudinal region, SG = Seagrass. 234

Figure 6.4 Densities of *Micrelenchus huttonii* vs. *Diloma nigerrimum* in four different habitats in the Avon-Heathcote Estuary. There was no significant relationship between the two snail taxa. Black and white symbols represent summer and winter samples, respectively. There were 36 samples (14% of collected cores) without any *Micrelenchus* or *Diloma*. 235

Figure 6.5 Mean densities (+SE) of *Diloma nigerrimum* and *Micrelenchus huttonii* in the Avon-Heathcote Estuary over (A) two seasons (summer n = 126, winter n = 127, each bar), (B) two sites (Plover n = 125, Tern n = 128, each bar), (C) two elevations (intertidal n = 128, subtidal n = 125, each bar), and (D) four habitats (bare n = 64, *Ulva* n = 61, seagrass n = 64, seagrass+*Ulva* n = 64, each bar). Samples were taken with benthic cylindrical cores, 9 cm diameter × 10 cm depth). SG = Seagrass bed. Note the different scales and breaks in the axes of the plots. 236

Figure 6.6 Mean grazing rates (+SE) of the estuarine trochid snails *Diloma nigerrimum* and *Micrelenchus huttonii* in lab and field experiments over 10 days. (A) a no-choice lab experiment (n = 6) with no-snail control and 4 snail treatments of 2 or 10 snails of both taxa and one food to eat: the seagrass *Zostera*, the green seaweed *Ulva*, or the red seaweed *Gracilaria*. (B) a snail-choice lab experiment (n = 6) only using the 10 snail treatments of both snails, with the addition of sediment (S), and a treatment including both *Ulva* and *Gracilaria* (U+G). The seaweed being examined is in parentheses after the treatment; i.e. U+G (G) is examining grazing rates of *Gracilaria* in the *Ulva+Gracilaria* treatment. (C) a food choice field experiment (n = 5) using only 10 *Micrelenchus*. Negative values equate to grazing, positive values equate to seaweed biomass growth. 237

Figure 6.7 Size distributions (mm) and epibionts on the trochid snail *Diloma nigerrimum* and *Micrelenchus huttonii* in the Avon-Heathcote Estuary. (A) Size distribution of *Diloma* (bars, in mm, n=1543) and percent of epiphytized snails in each size class (points and line). (B) Mean ± SE number of epibionts found in each shell size category of *Diloma*. (C) Mean (+SE) richness of epibionts from each size category of *Diloma* shell sizes. (D) Size distribution of *Micrelenchus* (bars, in mm, n=11939) and percent of epiphytized snails in each size class (points and line). (E) Mean (+SE) number of epibionts found in each *Micrelenchus* shell size category. (F) Mean (+SE) richness of epibionts from each *Micrelenchus* size category. All snail shell sizes are lengths from bottom of aperture to top of spire. 238

Chapter 7

Figure 7.1 Proportion of collected samples with sessile (grey bars) and mobile (black bars) estuarine foundation species found in isolation or co-occurring. SG = seagrass, SW = seaweed, DS = dead shells, Dn = *Diloma nigerrimum*, Mh = *Micrelenhcus huttonii*, from three latitudinal regions North (sessile N = 539, mobile N = 169 samples), Central (sessile N = 270, mobile N = 49), and South (sessile N = 525, mobile N = 160). 252

Figure 7.2 Synthesis of foundation species' effects between each other and benthic estuarine communities as described in this thesis. The direction of the arrow indicates the relationship, with the arrow point describing the recipient of the effect. Facilitative effects = red, negative effects = blue, no effect = black, while multiple arrows indicate variable effects (indicative of arrow colours) from different studies within this thesis. Facilitative effects include responses such as habitat-formation or nutrient inputs, while negative effects can include grazing or competition. Gc = *Gracilaria chilensis*,

Usp. = *Ulva* spp., Zm = *Zostera muelleri*, As = *Austrovenus stutchburyi*, DS = dead shells, Dn = *Diloma nigerrimum*, and Mh = *Micrelenchus huittonii*. Graphics used are from Integration and Application Network, University of Maryland Center for Environmental Science, as well as by the author. 253

LIST OF TABLES

Chapter 3

Table 3.1 ANOVA testing for effects of latitudinal region (north, central, south) and estuaries (15) on arcsine square-root transformed percent cover of (A) seagrass and (B) seaweed (n = 90, except one estuary were n = 76). Alpha was reduced to 0.01 because variances could not be transformed to homogeneity. Significant effects are in bold. 94

Table 3.2 ANOVA testing for effects of year (2014/15 vs 2015/16), season (summer vs. winter), and site (Plover vs. Tern street) on arcsine square-root transformed percent covers of (A) seagrass and (B) seaweed in the Avon-Heathcote Estuary. Alpha was reduced to 0.01 because variances could not be transformed to homogeneity. Significant effects are in bold. 95

Table 3.3 ANOVA testing for effects of latitudinal region (north, central, south), estuary (15), elevation (intertidal, subtidal) seagrass (presence-absence) and seaweed (presence-absence) on (A) density (log 10+1 transformed) and (B) richness of shell-forming bivalves and snails in sediment cores (9 cm diameter × 10 cm depth, n = 3). Significant effects are in bold. 96

Table 3.4 ANOVA testing for effects of year (2014/15 vs 2015/16), season (summer vs. winter), and site (Plover vs. Tern street) on (A) density (log 10+1 transformed) and (B) richness of shell forming snails and bivalves, in the Avon-Heathcote Estuary in sediment cores (9 cm diameter × 10 cm depth, n = 4). Significant effects are in bold. Significant effects are in bold. 98

Table 3.5 Experiment 1. ANOVA testing for effect of manipulated amounts of seagrass (control, cut, removed), mussels (adding 0, 1, 4), and *Ulva* seaweed (adding 0, 150, 500 mL) on (A) density and (B) richness of shell forming snails and bivalves in the Avon-Heathcote Estuary in sediment cores (9 cm diameter × 10 cm depth, n = 4). Significant effects are in bold. 101

Table 3.6 Experiment 1. ANOVA testing for effect of manipulated amounts of seagrass (control, cut, removed), mussels (adding 0, 1, 4), and *Ulva* seaweed (adding 0, 150, 500 mL) on (A) seagrass root biomass and (B) seaweed biomass (pooling across the *Ulva* test factor) in the Avon-Heathcote Estuary in sediment cores (9 cm diameter × 10 cm depth, n = 4). Significant effects are in bold. 102

Table 3.7 Experiment 2. ANOVA testing for effect of manipulated amounts of seagrass (control, cut, removed) and *Ulva* seaweed (adding 0, 150, 500 mL) on (A) density and (B) richness of shell forming snails and bivalves in the Avon-Heathcote Estuary (n = 3). Significant effects are in bold. 103

Table 3.8 Experiment 2. ANOVA testing for effect of manipulated amounts of seagrass (control, cut, removed) and *Ulva* seaweed (adding 0, 150, 500 mL) on (A) seagrass leave biomass (only for the control seagrass plots), (B) seagrass root biomass and (C) seaweed biomass (pooling across the *Ulva* test factor) in the Avon-Heathcote Estuary (n = 3). Significant effects are in bold. 104

Chapter 4

Table 4.1 ANOVA testing for effects of latitudinal region (north, central, south) and tidal elevation (low, high) on (A) habitat interactions, (B) richness of habitat-formers, and (C) richness of habitat-users. Twelve quadrats (0.010 m^2) were sampled in each of 14 estuaries on the South Island of New Zealand. Significant effects are in bold. 143

Table 4.2 ANOVA testing for effects of habitat (mud, silt, sand, seagrass) and elevation (low, high) on (A) habitat interactions, (B) richness of habitat-formers, and (C) richness of habitat-users (log 10 transformed) in the Avon-Heathcote Estuary. This survey was done with large quadrats (0.0625 m^2, silty sites n = 21, sandy, muddy and seagrass sites n = 14). Significant effects are in bold. 144

Table 4.3 ANOVA testing for diurnal effects (day, night) on (A) habitat interactions involving mobile organisms, (B) richness of mobile habitat-formers, and (C) richness of mobile habitat-users. This

survey was done with small quadrats (0.010 m^2, n = 8) near Plover street in the Avon-Heathcote estuary. Significant effects are in bold. 145

Table 4.4 ANOVA testing for effects of quadrat size (0.0625 m^2, 0.010 m^2) and habitat (mud, dead shells, seagrass) on (A) habitat interactions, (B) richness of habitat-formers, and (C) richness of habitat-users. This survey was done near Tern Street in the Avon-Heathcote estuary (n = 3 per combination of quadrat size and habitat). Significant effects are in bold. 146

Chapter 5

Table 5.1 ANOVA table for of percent cover of surface-dwelling dead shells (Arcsine square-root transformed) from (A) a latitudinal survey of 6 estuaries from 3 regions, (B) a spatial 2014 survey in the Avon-Heathcote Estuary in 2 habitats (silty sites vs. seagrass sites, 4 sites) and 2 sites, and (C) a two-year seasonal survey from the Avon-Heathcote Estuary (summer vs. winter, 2 sites). Alpha was reduced to 0.01 in all tests because variance homogeneity could not be confirmed. Significant effects are in bold. 182

Table 5.2 ANOVA table for invertebrate (A) density (m^{-2}, log 10+1 transformed), (B) taxonomic richness ($quadrat^{-1}$, log 10+1 transformed), and (C) multivariate community structure from a 2014 spatial survey in three habitats around the Avon-Heathcote Estuary. Shell = presence-absence of shells; Habitat = bare (unvegetated) sediments, the seagrass *Zostera muelleri*, and the seaweed *Ulva* spp. Significant effects are in bold. 183

Table 5.3 Dissimilarity table (SIMPER test) of invertebrate communities between quadrats where shells were either present or absent in a survey in the Avon-Heathcote Estuary. Listed are taxa that explain 82.2% of the dissimilarity between the two communities, with each organism's contribution also listed. The total overall dissimilarity between the shell-present and shell-absent communities was 80%. 184

Table 5.4 ANOVA table for invertebrate (A) density (m^{-2}, log 10+1 transformed), (B) taxonomic richness, (C) multivariate community structure, and on seaweed (D) densities (m^{-2}, log 10+1 transformed)) and (E) richness (log 10+1 transformed) recruited to out-transplanted shells, from an experiment conducted in six estuaries from three regions (North, Central, South) on the South Island of New Zealand. Shell = presence/absence of shells (adding 10-15 shells per plot). Habitat = bare sediments, seagrass habitat with leaves cut, and undisturbed natural seagrass. Note that seaweed responses were only relevant to test in shell addition treatments (and therefore excluded the Shell-test factor). Significant effects are in bold. 185

Table 5.5 Dissimilarity table (SIMPER test) of invertebrate communities between plots with or without added shells in a latitudinal experiment in six estuaries. Listed are taxa that explain 77.6% of the dissimilarity between the two communities, with each organism's contribution also listed. The total overall dissimilarity between the shell-present and shell-absent communities was 87%. 186

Table 5.6 ANOVA table for (A) seagrass leaf biomass, (B) seagrass root biomass (log 10+1 transformed), and (C) shell retention (arcsine square-root transformed), from an experiment conducted in six estuaries from three regions (North, Central, South) on the South Island of New Zealand. Shell = presence-absence of shells (adding 10-15 shells per plot). Habitat = bare sediments, seagrass habitat with leaves cut, and undisturbed natural seagrass. Note that seagrass responses were only relevant to test in the seagrass habitat (and therefore excluded the bare mud habitat), whereas the shell retention response only was relevant to test in the shell addition treatment (and therefore excluded the Shell-test factor). Significant effects are in bold. 187

Chapter 6

Table 6.1 ANOVA tables of densities of (A) *Diloma nigerrimum* (log 10 +1 transformed), and (B) *Micrelenchus huttonii* (log 10 +1 transformed), from a latitudinal survey of 15 estuaries from 3

regions (North, Central, South) on the South Island of New Zealand. Additional orthogonal test factors included tidal elevation (intertidal vs. subtidal), presence and absence of seagrass (± SG) and presence and absence of seaweed (± SW). Densities of *Diloma* and *Micrelenchus* were correlated (see Figure 3) so separate analyses were done for the two taxa. Significant effects are in bold. 225

Table 6.2 ANOVA table of snail densities found from a temporal survey in the Avon-Heathcote Estuary over two years. Examined orthogonal test factors include snail taxa (*Diloma nigerrimum* and *Micrelenchus huttonii*), seasons (summer, winter), sites (Plover St. closer to river mouth, vs. Tern St. closer to ocean entrance), tidal elevations (intertidal vs. subtidal), presence or absence of seagrass (± SG) and presence or absence of seaweed (± SW). Alpha was reduced to 0.01 for this test because of variance heterogeneity. Densities of *Diloma* and *Micrelenchus* were not correlated (see Figure 5), so Taxa was added as an orthogonal test factor. Significant effects are in bold. 227

Table 6.3 ANOVA table examining grazing rates in various experiments in (A) Laboratory with no-choice of food (either *Zostera*, *Gracilaria*, or *Ulva*), for *Diloma nigerrimum* and *Micrelenchus huttonii* (taxa) in two abundances 2 or 10 snails, plus control. (B) Laboratory experiment with food choice (*Ulva*, *Gracilaria*, or *Ulva+Gracilaria*), with +/- 2 cm of sediment added for 10 snails of *Diloma* and *Micrelenchus*. Alpha was reduced to 0.01 for this test as variance homogeneity could not be confirmed. (C) Field experiment with food choice (*Ulva*, *Gracilaria*, or *Ulva+Gracilaria*) for 10 *Micrelenchus* snails. 229

Table 6.4 Mean (± SE) length (mm) and epibiont abundances (per shell) attached to the trochid snails *Diloma nigerrimum* (*n*=1543, 661 snails with at least one epibiont) and *Micrelenchus huttonii* (*n*=11939, 6751 snails with at least one epibiont) in the Avon-Heathcote Estuary. Total = number of shells inhabited by a specific epibiont. * = calculated from presence-absence only. 230

Table 6.5 Two-way ANCOVA table, with Size as a covarying factor, examining (A) epibiont abundance and (B) epibiont taxa richness found on two snail taxa (*Diloma nigerrimum* and *Micrelenchus huttonii*), and two examination methods (stereoscope and naked eye). Alpha was reduced to 0.01 for both tests as variance homogeneity could not be confirmed even after attempted transformations. Significant effects are in bold. 231

CHAPTER 1 GENERAL INTRODUCTION

Overview of foundation species

Many ecosystems and habitats around the world, such as mangroves, coral reefs, forests, and seagrass beds, exist because of habitat-forming species that have a widespread effect on biotic and abiotic functions (Carlton 1974, Jones et al. 1994, Ellison et al. 2005, Orth et al. 2006, Hastings et al. 2007). These critical organisms that define the structure of a community due to habitat creation, competitive domination, and/or disturbances are known as foundation species (Dayton 1972). Foundation species enhance the habitat around them by modifying physical conditions, mediating biotic interactions, maintaining or increasing biodiversity, and reducing environmental stress (see Paine and Vadas 1969, Dodson 1970, Dayton 1972, Mills et al. 1993, Power et al. 1996, Ricciardi et al. 1997, Diaz and Rützler 2001, Ellison et al. 2005, Angelini et al. 2011, Schmidt et al. 2011, Altieri and Witman 2014). One of the most widespread and common ecological function of foundation species is formation of habitat that support other organisms, a process also referred to as 'autogenic ecosystem engineering' (Jones et al. 1997). The above ecological functions are common in terrestrial (e.g., trees, cacti, shrubs), freshwater (e.g., bivalves, macrophytes), and marine (e.g., mangroves, seagrasses, seaweed, mussel, oysters) systems.

In marine systems, estuaries are often dominated by foundation species. Estuaries are characterized by unstable low-relief sedimentary mud and sand flats (Knox et al. 1973, Jupp et al. 2007), where sediment grain size, tidal exposure, and changes in salinity are important factors that determine the composition of benthic communities (Smith and Duke 1987, Rodrigo 1989, Thrush et al. 2003). Foundation species can add physical structure to these homogenous sedimentary systems and transform them into biodiversity hotspots. Most estuaries are inhabited by at least four general types of foundation species: slow-growing clonal seagrasses (e.g., *Zostera muelleri*), fast-growing seaweeds (e.g., *Gracilaria chilensis* and *Ulva* spp.), sessile filter-feeding shell-forming animals (such as the bivalve *Austrovenus stutchburyi*) and mobile slow-moving shell-forming animals (snails like *Micrelenchus huttonii* and *Diloma nigerrimum*) (Figure 1.1). Other organisms may not be common in some estuaries but may still function as foundation species, such as chitons, urchins, sponges, tunicates, and decorator crabs.

Seagrasses as foundation species

Seagrasses are marine angiosperms that are mainly perennial (Kuo and den Hartog 2006) and are prime examples of foundation species (Hughes et al. 2008, Franssen et al. 2011, Thomson et al. 2015). Seagrasses grow in patches (beds) within the photic zone, across shallow coastal and estuarine landscapes, and are relatively permanent features of the landscape. Patches vary in density, shape and size, and can grow or shrink from season to season (Harrison and Mann 1975, Zieman et al. 1999, Boström et al. 2006). Bed maintenance and expansion occur through sexual reproduction (flowering) and clonal belowground rhizome expansion (Olesen et al. 2004, Rasheed 2004, Duarte et al. 2006). Seagrass beds are among the most photosynthetically productive communities on Earth (27.4 Tg C $year^{-1}$), and act as important carbon sinks ('blue carbon sink') to mitigate global climate change effects (Duarte and Chiscano 1999, Fourqurean et al. 2012). Seagrass beds are therefore economically important, providing ecosystem services estimated worth of ca. US (2007) \$28,916 $hectare^{-1} \cdot year^{-1}$ globally (Costanza et al. 2014).

Seagrasses are important in estuarine environments both above and below the sediment surface. Below the sediment surface, seagrasses bind and stabilizes sediment particles with their rhizomes and roots (den Hartog 1970, Orth 1977, Marbà et al. 2006). Above the sediment surface, seagrass leaves add a physical three-dimensional habitat that reduces water flows, allowing nutrients, sediments, and juvenile organisms to settle out in the seagrass bed (Fonseca and Cahalan 1992, Boström et al. 2006, Connolly and Hindell 2006). Seagrasses also support entire communities of associated plants and animals and are particularly important as a nursery habitat for many juvenile invertebrates and fish (Reusch and Chapman 1995, Grizzle et al. 1996, Nagelkerken et al. 2000, Beck et al. 2001, Orth et al. 2006, van der Heide et al. 2007, Battley et al. 2011).

Seagrass can also occur on rocky shores, although fewer taxa are adapted to this habitat (Cooper and McRoy 1988, Kuo and den Hartog 2006). The leaves of seagrass on rocky shores act in a similar manner to those in estuaries: they provide a physical buffer for waves and increase biodiversity by adding habitat complexity for intertidal communities (Turner 1985, Woods and Schiel 1997, Tuya et al. 2010).

Seaweeds as foundation species

Macroalgae (seaweed) are more fragile and ephemeral than seagrasses, but still provide important functions such as habitat-formation, a food-source, and stress reduction (i.e. reduce desiccation during low tide) (Dudgeon and Petraitis 2005, Dijkstra et al. 2012, Bishop et al. 2013, Ramus et al. 2017, Thomsen et al. 2018b). Seaweeds can be ephemeral, such as filamentous *Cladophora* and sheet-forming *Ulva* spp., or long-lived perennials, such as the intertidal rockweed *Ascophyllum nodosum* and the giant kelp *Macrocystis pyrifera*. Perennial seaweed beds typically build more stable beds compared to ephemeral species.

Seaweeds in sedimentary systems such as estuaries, provide habitat, a food-source and can reduce environmental stress. For example, branching perennial red algae like *Gracilaria* spp. are common in many estuaries around the world where they provide habitat and increase diversity of benthic invertebrates (Cardoso et al. 2004, Thomsen et al. 2009a, Thomsen et al. 2010a, Byers et al. 2012, Thomsen et al. 2013, Wright et al. 2014, Munari et al. 2015). Ephemeral seaweeds, like *Ulva* spp. can also function as foundation species. *Ulva* is an opportunistic and fast growing seaweed, that often inhabit eutrophic areas with high nutrient loading (Harlin and Thorne-Miller 1981, Valiela et al. 1997, Raffaelli et al. 1998, Barr et al. 2013, Ren et al. 2014). *Ulva* can bloom however, quickly generating large amounts of biomass that form thick, drifting, algal mats that can cover entire estuaries, reducing available light for primary producers below the mats, can change water chemistry, and create hypoxia in the sediments, affecting invertebrate survival and behaviour (Thiel et al. 1998, Brun et al. 2003b, Sugimoto et al. 2007, Marsden and Bressington 2009, Mvungi et al. 2012). However, *Ulva* can, like many other drift algae, also facilitate invertebrates that use its structure above the sediments by providing habitat (which also provides refuge from predation and environmental stress), and food (Wilson et al. 1990, Geertz-Hansen et al. 1993, Cardoso et al. 2004, Powers et al. 2007, Thomsen and Wernberg 2015) when found in lower abundances and densities.

Seaweeds are also important foundation species on rocky shores. For example, the long-lived fucoid alga *Ascophyllum nodosum* is a dominant competitor for space in the low intertidal zone in the northern hemisphere (Dudgeon and Petraitis 2005). *Ascophyllum* beds provide habitat and refuges from environmental stressors and predation, and act as a source of food (Bertness et al. 1999, Pavia et al. 1999, Schmidt et al. 2011, Phillippi et al. 2014). Similarly, in New Zealand, fucoid perennial algae such as *Hormosira banksii* and *Cystophora torulosa*

increase biodiversity of both fauna and other algae, and act as refuges for other fucoid recruits on rocky shores (Lilley and Schiel 2006, Schiel 2006, Schiel and Lilley 2011).

Bivalves as foundation species

Foundation species are not only primary producers but can also be primary consumers. Shell-forming bivalves are particularly important foundation species in marine and freshwater systems (Beukema 1982, MacIsaac 1996, Gutiérrez et al. 2003). Shell-formers create a complex and heterogeneous structure on, and in, benthic sediments and produce substantial amounts of shell-material (50 to 1000 $g \cdot m^{-2} \cdot year^{-1}$ for most molluscs) that last for prolonged periods even after death of the organism (Beukema 1982, MacIsaac 1996, Gutiérrez et al. 2003).

Bivalves are important foundation species on many rocky shores. For example, beds of dominant bivalve competitors, like the California mussel *Mytilus californianus* and the blue mussel *Mytilus edulis* (Menge 1976, Lubchenco and Menge 1978, Suchanek 1992, Altieri and Witman 2006), support high biodiversity by providing refuge (both environmental and predatory), food, and complex habitat (Suchanek 1992, Peake and Quinn 1993, Borthagaray and Carranza 2007, Norling and Kautsky 2007).

In estuaries, oysters can create consolidated beds and reefs up to 1000 m^2 of hard substrate (Coen and Luckenbach 2000), which increase invertebrate diversity (Lehnert and Allen 2002, Gain et al. 2016, Hanke et al. 2017), enhance nutrient cycling (Dame et al. 1985, Dame et al. 1989), increase filtration of the water column (Coen et al. 2007, Grabowski and Peterson 2007), and stabilize sediments (Henderson and O'Neil 2003, Grabowski and Peterson 2007). However, bed-forming gregarious mussels and oysters, are not the only bivalves that function as foundation species. Solitary bivalves, such as the cockle *Cerastoderma edule* facilitate polychaetes and amphipods due to increased sediment accumulation (Donadi et al. 2015), and the clam *Anadara trapezia* support a diverse epibiotic community on its shell in *Caulerpa taxifolia* meadows in Australia (Gribben et al. 2009). The clam *Austrovenus stutchburyi* in New Zealand estuaries is commonly inhabited by attached seaweeds, such as *Gracilaria*, *Ulva* spp., and *Codium fragile* (pers. obs.) which can result in facilitation cascades (Thomsen et al. 2010a, Thomsen et al. 2016).

Mobile foundation species

Not all foundation species are sessile. For example, mobile shell- and test-forming snails, crustaceans, and echinoderms can also provide habitat and refuge for inhabitants (Gutt and Schickan 1998, Buschbaum and Reise 1999, Sandford 2003, Chan and Chan 2005, Linse et al. 2008, Ayres-Peres and Mantelatto 2010, Thomsen et al. 2010b, Thyrring et al. 2013). Although epibiosis associated with mobile shell-forming species is common in the fossil record (Palmer et al. 1993, Walker 1995, Nebelsick et al. 1997, Schneider 2003, Waugh et al. 2016), the study of mobile foundation species as present day habitat-providers has received much less scrutiny compared to sessile foundation species. However, in Antarctica biogenic hosts support diverse epibiotic communities, with more than 370 epibiotic relationships between sessile and mobile organisms (Gutt and Schickan 1998, Linse et al. 2008). In this system, is has been shown that urchins alone provide substratum for at least 51 species (from 10 taxonomic classes), increasing the overall diversity of these cold water communities (Gutt and Schickan 1998, Linse et al. 2008). Similarly, Altieri and Witman (2014) found that in the Galapagos Islands, the spines of the slate-pencil urchin (*Eucidaris galapagensis*) provided stable substrate and predation refuge, its spines being covered by more than 20 epibiotic taxa. Snails, such as *Turbo torquatus*, can also be mobile foundation species, often being inhabited by foliose and coralline algae and limpets (Wernberg et al. 2010). Similarly, *Battilaria* spp. and *Littorina littorea* also create hard substrate that function as attachment space for barnacles, polychaetes, oysters, and algae, often increasing biodiversity of sessile organisms in sedimentary estuaries (Buschbaum and Reise 1999, Chan and Chan 2005, Thieltges and Buschbaum 2007, Thyrring et al. 2013).

Legacy effects of foundation species

Almost all studies on foundation species focus on when they are alive, but many foundation species can influence ecosystem functions and affect community structures of inhabitants even after they have died (Hastings et al. 2007, van de Voorde et al. 2011, Waldbusser et al. 2011). These continued effects have been referred to as ‘legacy effects’ (Molina and Amaranthus 1991, Cuddington 2011) or ‘taphonomic feedbacks’ (Kidwell and Jablonski 1983, Kidwell 1986, Powell et al. 2006). These legacy effects can last for days, months, or even centuries after the organism’s death, and can have wide ranging effects from communities to landscape scales (Hastings et al. 2007). Trees are probably the best-known organisms that leave long-lasting structural legacy effects because their branches, trunks and

roots provide habitat and food for birds and decomposers (Harmon et al. 1986, Franklin et al. 1987, Bunnell et al. 2002), alter stream flows and pathways (Sedell and Froggatt 1984, Abbe and Montgomery 1996), and can act as nursery plants for other flora (Maser et al. 1979, Harmon et al. 1986), for years, decades or even centuries. Mobile habitat-altering organism, like beavers, can also leave legacy effects. Beavers modify the landscape by transforming a flowing river system into a wetland that can persist for centuries, even if the beavers become locally extinct (Jones et al. 1994). In marine systems, dead seaweed (macroalgae) and seagrass can provide legacy effects, such as when beach-cast seaweed wracks provide food and habitat for invertebrates and birds for days, weeks or month after the organisms have died (i.e., being an example of a 'trophic legacy' effect, Figure 1.2) (Colombini and Chellazi 2003, Dugan et al. 2003, Rodil et al. 2008, Olabarria et al. 2010). Calcifying, reef-forming organisms such as corals, mussels, polychaetes and oysters are organisms that increase biodiversity and habitat heterogeneity, but these reefs would be much less prevalent without previous generations dying off to create substrate for juveniles to settle on (Bak 1976, Schuhmacher 1977, Abbe 1988, Hall-Spencer and Moore 2000, Gain et al. 2016). Bivalves are a particularly important legacy species, because they produce massive amounts of hard substrate (up to 90,000 g shell material m^{-2} $year^{-1}$), that can last for millions of years in fossil deposits (Kidwell 1986, Gutiérrez et al. 2003, Hastings et al. 2007). Bivalve beds and adjacent dead shells influence benthic communities, often increasing biodiversity and abundance of aquatic organisms around them compared to the surrounding areas (Figure 1.2) (Ricciardi et al. 1997, Posey et al. 1999, Gutiérrez et al. 2003, Schejter and Bremec 2007).

Interactions between coexisting foundation species

Foundation species do not exist in isolation but typically co-occur with other foundation species. For example, most forests are composed of many co-occurring tree, shrub, and epiphyte species (Nadkarni 1994, Kappelle et al. 1995, Leuschner et al. 2009, Nadrowski et al. 2010, Watson and Herring 2012) and coral reefs are composed of co-occurring hard and soft corals, sponges, giant clams, and echinoderms (Sammarco 1982, Diaz and Rützler 2001, Burkepile and Hay 2008). Similarly, co-occurring and interacting foundation species are common in marine intertidal systems, typically being composed of a complex mix of seaweed, mussels, barnacles, and snails (Sousa 1984, Bertness and Leonard 1997, Albrecht 1998, Buschbaum and Reise 1999, Buschbaum and Saier 2001, Schmidt et al. 2011).

When foundation species co-occur, they often have enhanced positive effects on habitat-using species (*i.e.* facilitation cascades) (Altieri et al. 2007, Thomsen et al. 2010a, Bishop et al. 2013, Yakovis and Artemieva 2017). For example, Altieri et al. (2007) found evidence of a facilitation cascade on a New England cobblestone beach. They found, like previous studies (Bertness 1984), that the cordgrass *Spartina* facilitated the mussel *Geukensia* due to their root/rhizome structure that stabilized sediments and their canopy that buffered wave exposure but also that blue mussels, barnacles, algae, snails, and amphipods were additionally facilitated by *Geukensia*. Thus, *Spartina* was the primary foundation species that provided habitat for *Geukensia,* that subsequently provided additional physical habitat and interstitial space for smaller invertebrate communities (Altieri et al. 2007). Foundation species can coexist in adjacent or nested assemblages (Angelini et al. 2011). Adjacent foundation species assemblages, often found on larger landscape scales, typically develop when a primary competitively dominant foundation species uses all of the available substrate and does not allow for a secondary foundation species to use the interstitial spaces, creating zonal patches of foundation species (Angelini et al. 2011). For example, on Panamanian coasts, three types of mangrove trees dominate (the black mangrove *Avicennia germinans,* the white mangrove *Laguncularia racemose,* and the red mangrove *Rhizophora mangle*) forming specific zones along the tidal gradient (Sousa et al., 2007). By comparison, a nested foundation species assemblage can establish when (a) a primary foundation species does not use all available substrate, allowing other foundation species to colonize and grow in interstitial spaces, or (b) when a primary foundation species provides novel substrate that is colonized by subsequent foundation species (Angelini et al. 2011). An example of the first type of nested assemblage would be mussels which can colonize interstitial space in seagrass beds, and lead to mixed patches of mussels and seagrass in coastal areas (Valentine and Heck 1993, Reusch et al. 1994, Bologna et al. 2005). The second type of nested assemblage can be demonstrated from bivalves such as *Austrovenus stutchburyi* or *Anadara trapezia* where part of their shell emerges from the sediments allowing colonization of the shell by many epibionts, increasing diversity (Gribben et al. 2009, Thomsen et al. 2016). This thesis will focus on the nested foundation species assemblages around estuaries in New Zealand, where many foundation species will occur in the same sample.

Seagrass-Seaweed interactions

As previously discussed, seagrass provide physical habitat, trap nutrients and sediments, and buffer against physical disturbances (Fonseca and Cahalan 1992, Orth et al. 2006, Battley et al. 2011). However, seagrass beds are in decline around the world, in due to habitat modifications, increased sediment loading, introduction of invasive species, and nutrient enrichment (Orth et al. 2006, Waycott et al. 2009). Yet, opportunistic seaweeds are often facilitated by the same stressors, thereby changing the competitive hierarchies between seagrass and seaweed (Figure 3) (Valiela et al. 1997, McGlathery 2001, Lyons et al. 2014). For example, opportunistic seaweeds have been shown to have much greater biomass in estuaries with high nitrogen loading, compared to estuaries with low nitrogen loads (Valiela et al. 1997, Hauxwell et al. 2001). These increases in seaweed biomass can lead led to toxic nutrient concentrations and shade seagrasses, which lead to decreased seagrass growth, loss of biomass, and possibly death (Hauxwell et al. 2001, McGlathery 2001, Nelson and Lee 2001, Brun et al. 2003a, van der Heide et al. 2008, Han and Liu 2014). However, seaweed may also facilitate seagrass, for example, by releasing dissolved organic carbon and other organic matter, by decreasing intertidal desiccation stress (Figure 1.3A) (Khailov and Burlakova 1969, Brun et al. 2003b, Wada et al. 2007). Seagrasses can also affect seaweeds (Figure 1.3A). For example, in the Mediterranean Sea the native seagrass *Posidonia oceanica* positively influenced the growth of the invasive green algae *Caulerpa taxifolia*, possibly by reducing water flow within the seagrass beds (Ceccherelli and Cinelli 1998, 1999). In Tanzania, Mtolera (2003) suggested that seagrass was able to contribute limiting metals to seaweeds thus increasing growth rate of seaweeds, as well as increasing seaweed defences and production. Seagrasses often also facilitated smaller, epiphytic seaweeds as its leaves provide attachment space (Saunders et al. 2003, Lobelle et al. 2013). Furthermore, seagrass can enhance nutrient availability to attached epiphytes by transportation of nutrients from substrate to leaf-surface and reduce water flow to trap drifting seaweed (Harlin 1975, Orth and Van Montfrans 1984, Grizzle et al. 1996, Lobelle et al. 2013), allowing the seaweed to remain in the photic zone instead of being transported to the shore or deeper trenches (Virnstein and Carbonara 1985).

Seagrass-Bivalve interactions

The interactions between seagrass and bivalves is potentially more complex and may vary between taxa and patch size and patch density. Seagrass habitats can provide multiple

positive benefits to bivalves (Figure 1.3B). Seagrass leaves reduce water currents which increase settlement of suspended sediments and planktonic bivalve larvae (Grizzle et al. 1996, Bologna and Heck 2000). Seagrasses can promote growth of bivalves such as *Argopecten irradians* and *Mercenaria mercenaria* on edges of patches, possibly due to increased deposition of organic matter (Peterson et al. 1984, Judge et al. 1993, Irlandi 1996, Bologna and Heck Jr. 1999). Seagrass have also been shown to increase survival of the mussel *Modiolus americanus* and the clam *Mercenaria mercenaria*, and dispersal and bed-creation of *Mytilus edulis* (Reusch and Chapman 1995, Irlandi 1997, Peterson and Heck Jr 2001b). However, other studies have shown that dense seagrass beds can have no or negative effects on growth of the *Mya arenaria*, *Mercenaria mercenaria*, and *Musculista senhousia* (Figure 1.3B) (Beal 1994, Irlandi 1996, Reusch and Williams 1998, Allen and Williams 2003). Such negative effects have been attributed to the seagrass beds providing a refuge for predators, such as crabs and juvenile lobsters, that nip on bivalve siphons (so that injured bivalves have to expend energy on siphon repair instead of growth) (Coen and Heck Jr. 1991, Rainer and Wadley 1991, Beal 1994, Irlandi 1994).

Bivalves can also affect seagrasses both positively and negatively, and may influence seagrass both from within and outside the bed (Figure 1.3B). Bivalves produce and deposit large amounts of organic matter through faeces and pseudo-faeces onto the sediments and into the water column (Dame et al. 1980), which can be converted to nitrogen and phosphorous and thereby increase seagrass growth (Dame et al. 1989, Reusch et al. 1994, Reusch and Williams 1998, Peterson and Heck Jr 1999, 2001a, Newell 2004). Bivalves can also reduce epiphytic load (and thus competition for light and nutrients) on seagrass leaves. In the Gulf of Mexico there was less epiphytic seaweed when the mussel *Modiolus americanus* was present in the seagrass beds, resulting in 10% more light availability (Peterson and Heck Jr 2001a, b). Bivalves can also increase light availability by filtering out plankton, even if bivalves are found outside seagrass beds (Newell and Koch 2004, Smith et al. 2009). One family of clams (Lucinidae) reduce stress on seagrass through symbiotic gill bacteria by oxidizing toxic sulphides (van der Heide et al. 2012). However, bivalves can also affect seagrass negatively (Figure 1.3B). For example, high levels of organic matter production may decrease oxygen levels (due to bacterial respiration) (Newell 2004, Vinther et al. 2008). In addition, fast growing epiphytes may be facilitated by bivalve nutrients, and thereby increase seagrass leaf shading (Williams and Ruckelshaus 1993, Vinther et al. 2008).

Finally, bivalves can physically occupy all sediment space and thereby inhibit growth and expansion of seagrass rhizomes and roots (Reusch and Williams 1998).

Seaweed-Bivalve interactions

Interactions between seaweeds and bivalves are, like interactions described in previous sections, also complex (Figure 1.3C) and may depend on the life history (ephemeral versus long-lived) and attachment status (free-floating versus attached with a holdfast) of the seaweeds (Holmquist 1994, Thiel et al. 1998, Jones and Pinn 2006). For example, drift seaweed can facilitate dispersal of benthic bivalves in some areas (Holmquist 1994, Ingólfsson 1995, Mistri et al. 2004). In Florida Bay, USA, seven taxa of bivalves were found in tumbling clumps of the red algae *Laurencia* spp., drifting up to 0.5 km·day^{-1} (Holmquist 1994).

Similarly, pelagic rafts of *Ascophyllum nodosum* and *Fucus* spp. were found to be inhabited by two bivalve species, possible having travelled hundreds of kilometres around Iceland (Ingólfsson 1995). Stationary seaweeds can also facilitate bivalves. On Brazil coastlines, native *Sargassum* spp. grow in dense stands on the intertidal zone, reducing desiccation and thermal stress of the invasive oyster *Isognomon bicolor* (López and Coutinho 2010) and in Australia, the invasive seaweed *Caulerpa taxifolia* can increase survival of the native clam *Anadara trapezia* by providing a refuge from predatory fish (Gribben and Wright 2006). In addition, seaweeds provide food (up to 66%, determined by isotopic analysis) for bivalves when the thallus breaks into small fragments (Kang et al. 1999, Xu and Yang 2007, Hondula and Pace 2014). However, more often, seaweed have negative effects on bivalves, particularly when opportunistic species bloom (Figure 1.3C). For example, in eutrophic estuaries (and typically during warm summer months) rapid growth of *Ulva, Enteromorpha, Chaetomorpha,* and *Cladophora* spp. form mats that smother the benthos, decrease oxygen levels, reduce water currents, and eventually cause die-offs of infauna (Everett 1991, Raffaelli et al. 1998, Thiel et al. 1998, Norkko et al. 2000, Cummins et al. 2004, Jones and Pinn 2006). Macroalgal mats may also cause clams such as *Mya arenaria*, *Austrovenus stutchburyi,* and *Arthritica helmsi* to live closer to the sediment surface to obtain food and oxygen, and thereby result in increased mortality from fish predation (Thiel et al. 1998, Auffrey et al. 2004, Cummins et al. 2004, Marsden and Bressington 2009). Seaweed attached to bivalves can also reduce the hosts filtration capacity and thereby its growth and survival. For example, Dittman and Robles (1991) found that epiphytic red algae decreased growth and

reproduction of *Mytilus edulis*. Furthermore, attached seaweed also increases hydrodynamic drag and can result in dislodgement and transport to the wrack zone (Dayton 1973, Witman and Suchanek 1984, Black and Peterson 1987, O'Connor et al. 2006).

Effects of bivalves on seaweeds have rarely been studied, although their shells, such as the invasive oyster (*Crassostrea gigas*) beds in Patagonia (Figure 1.3C) provide important attachment space for several species of red algae (Croce and Parodi 2012). In addition, bivalves, like *Mytilus trossulus*, may, through deposits of faeces and pseudofaeces, stimulate seaweed growth (Kotta et al. 2009) (and this study found no effect of habitat created by the mussels). A single study has shown negative effects of bivalves on seaweeds, as organic deposits from mussels inhibited growth of *Fucus serratus* embryos, probably because the organic matter increased hydrogen sulphide levels (Figure 1.3C) (Chapman and Fletcher 2002).

Seagrass-Seaweed-Bivalve interactions

Finally, it is possible that seagrass, seaweed and bivalves all co-occur in nested assemblages with even more complex direct and indirect positive and negative interactions (Orth and Van Montfrans 1984, Vinther et al. 2008, Wall et al. 2011, van der Heide et al. 2012, Thomsen et al. 2013). For example, seagrass beds are diverse habitats where epiphytic algae can be attached to the leaves, invertebrates and fish inhabit space between and above the leaves, and bivalves inhabit the substrate in-between and below the leaves (Orth 1977, Orth and Van Montfrans 1984, Bologna and Heck Jr. 1999, Peterson and Heck Jr 2001b, Nakaoka 2005, Boström et al. 2006, Orth et al. 2006, Mvungi 2011, Lobelle et al. 2013). In the Mediterranean Sea it has been shown that the alga *Lophocladia lallemandi* often is attached to the shells of the mussel *Pinna nobilis* which typically grows in between seagrass leaves (Box et al. 2009). Thus, the seagrass provides habitat for both algae and bivalves, and the bivalves again provides substrate for more algae. To date, only one study has experimentally quantified interactive effects between these three types of foundation species and associated invertebrate communities, showing that the seagrass *Zostera marina* provides habitat for the alga *Gracilaria vermiculophylla* and mussel *Mytilus edulis* to facilitate invertebrates through supplementary ecosystem functions (Thomsen et al. 2013).

Main study areas

My research was done in 15 estuaries around the South Island of New Zealand, with emphasis on the Avon-Heathcote Estuary in Christchurch (Figure 1.4). The Avon-Heathcote Estuary is an approximately 7 km^2 shallow, bar-built, triangular-shaped water body (Knox et al. 1973, Jupp et al. 2007). The Avon-Heathcote was covered by c. 2.1 km^2 firm intertidal mud and sand flats in 2002, but liquefaction and sediment mixing following earthquakes in 2010 and 2011, coupled with leaking of raw-sewage (Knox et al. 1973, Jupp et al. 2007, Measures et al. 2011) decreased firm mud and sand to ca. 1.8 km^2 in a 2016 benthic survey (Hollever and Bolton-Ritchie 2016). Dead shell banks comprise about 0.5 km^2 of sediments (Hollever and Bolton-Ritchie 2016). The 4 km long New Brighton Spit encloses the east side of the estuary. Seagrass beds along the spit cover ca. ca. 0.35 km^2 (Hollever and Bolton-Ritchie 2016). The rest of the estuary is comprised of various mixtures and firmness of sand (firm: 0.64 km^2, mobile: 0.39 km^2), mud (mobile firm mud/sand: 0.54 km^2, mobile soft mud/sand: 0.10 km^2, soft mud: 0.65 km^2, very soft mud/sand: 0.56 km^2), silts, and stones (Hollever and Bolton-Ritchie 2016). Two rivers, the Avon from the north and Heathcote from the southwest, flow into the estuary, and continue to carve channels throughout the estuary towards the ocean. Sediment grain sizes (<63 µm = silt, 63-125 µm = very fine sand, 125-250 µm = fine sand, >250 µm = medium sand) were typically smaller near the river entrances (Avon River: ca 20% silt, 15% very fine sand, 60% fine sand, 5% medium sand, Heathcote River: ca. 25% silt, 23% very fine sand, 43% fine sand, 9% medium sand) and near the Oxidation Ponds (ca. 38% silt, 18% very fine sand, 43% fine sand, 1% medium sand), while larger grain sizes were found more on the eastern spit side (End of spit near ocean: ca. 10% silt, 19% very fine sand, 70% fine sand, 1% medium sand, Heron Street (north of Plover Street): ca. 5% silt, 10% very fine sand, 79% fine sand, 6% medium sand (Skilton 2013) (Figure 1.4). The estuary is well-flushed with most of its water draining during low tide (Knox et al. 1973). The lunar tides have a typical range of 1.7 m at neap tide to 2.2 m at spring tide (Knox et al. 1973) but are also influenced by wind, atmospheric pressure and waves.

Like other estuaries (Vernberg 1976, Hinchey et al. 2006, Wilson and Fleeger 2012) the Avon-Heathcote Estuary has a strong salinity gradient from the two rivers to the ocean. The low salinity near the rivers cause osmotic stress for marine organisms, although many estuarine species can tolerate salinity fluctuations (Jones and Simons 1982, Marsden 2004). In the estuary salinity ranges from ca. 8-12 ppt around the mouth of the Heathcote River to

ca. 20-29 ppt near the Oxidation Ponds (Figure 1.4) (Marsden 2004). Similarly, salinity varies from 8-15 ppt near the Avon to c. 22-30 ppt near New Brighton Spit and the estuary mouth (Figure 1.4) (Marsden 2004). Sediment are typically exposed to atmospheric conditions for 3-5 hours during low tides, although there are many water-filled pools and channels (McClatchie et al. 1982). In addition to the salinity and desiccation gradients, heavy metal concentrations (Purchase and Fergusson 1986, Rodrigo 1989, Marsden et al. 2014), nutrient and organic matter loadings (Bolton-Ritchie and Main 2005, Marsden and Baharuddin 2015) and turbidity (Roper et al. 1983) also vary throughout the estuary.

Thesis outline

The overall objective of this thesis is to determine co-occurrence patterns and interactions between estuarine foundation species and their effects on associated communities along spatio-temporal gradients (Figure 1.5). Estuaries are a favourable model system for this objective as they are usually easily accessible, contain many environmental stressors and gradients (tidal, desiccation, sediment types), and the four main-types of foundation species (seagrass, seaweeds, bivalves, mobile shell-formers) co-occur and interact. Due to the three-dimensional nature of soft-sediments in estuaries, there are many organisms that live deep in the sediments (such as the bivalve *Macomona liliana* and many polychaetes), outside of the range of my sediment cores, thus my samples underestimate much of the infaunal community.

In Chapter 2 I use meta-analyses and a quantitative review to analyse reciprocal effects between aquatic (marine and freshwater) macroalgae, angiosperms, and bivalves. These analyses identify research gaps and quantify the direction and magnitude of their interactions. I test the hypotheses that (i) angiosperms have positive effects on bivalves but negative effects on macroalgae, (ii) macroalgae have negative effects on bivalves and angiosperms, (iii) bivalves have positive effects on angiosperms and macroalgae, (iv) small foundation species are affected more strongly than large foundation species, and (v) latitude, experimental duration, aquatic ecosystem type, and experimental type have no consistent modifying effect on these interactions.

In Chapter 3 I quantify co-occurrence patterns between seaweed and seagrass in a large survey of 14 estuaries across three latitudinal regions on the South Island of New Zealand, and their effects on shell-forming taxa. I also examine in detail, in a single estuary, co-

occurrences between seagrass and seaweeds over two years at different seasons and elevation levels, and their effects on shell-forming organisms. I also test experimentally for interactions between seagrass, seaweed, and bivalves. I hypothesize that (i) seagrass, seaweeds and bivalves co-occur in all sampled estuaries, (ii) shell-forming organisms are present year-round in the two-year survey, (iii) impacts of seaweed, seagrass and mussels on shell-forming organisms and other invertebrates are density-dependent, and (iv) that mussels and seaweed facilitate and inhibit seagrasses, respectively.

In Chapter 4 I quantify, in detail, habitat-use of estuarine organisms within 14 estuaries and two tidal elevations, and (in a single estuary) in different habitats, elevations and time of day. Based on close-up field observations I classify organisms as habitat-formers and habitat-users (organisms attached to habitat-formers) and quantify the number of habitat-interactions. I hypothesize that the number of habitat-interactions, -formers, and -users would be higher (i) in northern rather than southern estuaries, (ii) at low rather than high tidal elevations, (iii) in seagrass beds compared to unvegetated sediments, (iv) in larger-sizes than in smaller-sized quadrats, and (v) in samples during night rather than day samples.

In Chapter 5 I investigate the role that two estuarine snails play as mobile foundation species in both top-down (grazing pressure) and bottom-up (habitat provision) perspectives from the Avon-Heathcote Estuary, and their distributions in 4 habitats, 2 tidal elevations, and across 14 estuaries around the South Island of New Zealand. This research is innovative as there is little research on mobile foundation species in general (focused almost exclusively on sessile organisms), and no research that looks at the duality of mobile foundation species within a single outlet, as usually they are concentrated into either a trophic study or epibiosis study. I distinguish between two co-occurring, morphologically similar, trochid snails (*Micrelenchus huttonii* and *Diloma nigerrimum*) as to which exerts higher grazing pressure in estuaries, and which is more important as a habitat-provider. I hypothesize that (i) *Micrelenchus* is more abundant than *Diloma* across estuaries, in the subtidal zone, and associated with seaweed, (ii) *Diloma* is more abundant in the intertidal zone and on bare sediments, (iii) both snail species are more abundant in summer than winter, (iv) *Micrelenchus* exerts higher grazing pressures than *Diloma* on seaweeds, (v) *Diloma* has, per shell, higher abundance and richness of epibiota than *Micrelenchus*.

In Chapter 6, I examine the distributions and legacy effects of a ubiquitous cockle's (*Austrovenus stutchburyi*) dead shells in 6 estuaries around the South Island of New Zealand.

I also look at percent cover of dead shells on sediments over a two-year survey in the Avon-Heathcote Estuary. In a spatial experiment in 6 estuaries, I examine effects on estuarine invertebrate communities via three habitat treatments: bare sediments, seagrass leaves cut to sediments, and natural density seagrass, and the addition of dead shells to half of each habitat treatment. I also investigate the effects of shells on seagrass growth, and the effects of seagrass on shell retention. This research is novel, as there is little examination of dead bivalve shells as important habitat formers (what little there is mostly examines oyster or zebra mussel shells), even though bivalve shells can persist for centuries. In this chapter, I hypothesize that surface-dwelling dead shells are (i) common across estuaries, latitudes, sampling sites, and seasons on the South Island of New Zealand, (ii) have a positive impact on invertebrate and seaweed recruit densities and richness compared to un-vegetated mudflats, and (iii) have a negative impact on seagrass, through 'competition' for space and scouring of leaves.

Finally, I conclude that most foundation species I found in my research, do coexist and interact within estuaries along stress gradients, and spatial and temporal scales. I documented research gaps within the scientific literature about interactions between angiosperms, seaweeds, and bivalves, and suggest that filling these gaps will add to the overall knowledge of these foundation species in aquatic environments. I also found that some organisms act as foundation species that are new or understudied but provide facilitative and/or negative effects such as snails, bryozoa, living bivalves, and dead bivalve shells. I finally suggest that examining habitat use in both broad-scale and fine-scale, will help to detect new foundation species that may be overlooked, but still important to their community.

Figures

Figure 1.1 Examples of the habitats created by estuarine foundation species in New Zealand: the seagrass *Zostera muelleri* (A, B), the seaweeds *Ulva* spp. (C) and *Gracilaria chilensis* (D), and shell-forming organisms like the cockle *Austrovenus stutchburyi* (E), the snail *Micrelenchus huttonii*, (F) and dead shell accumulations (G, H). Photos represent 1 m^2 except for A, E, and F. *Micrelenchus huttonii*, (F) and dead shell accumulations (G, H). Photos represent 1 m^2 except for A, E, and F.

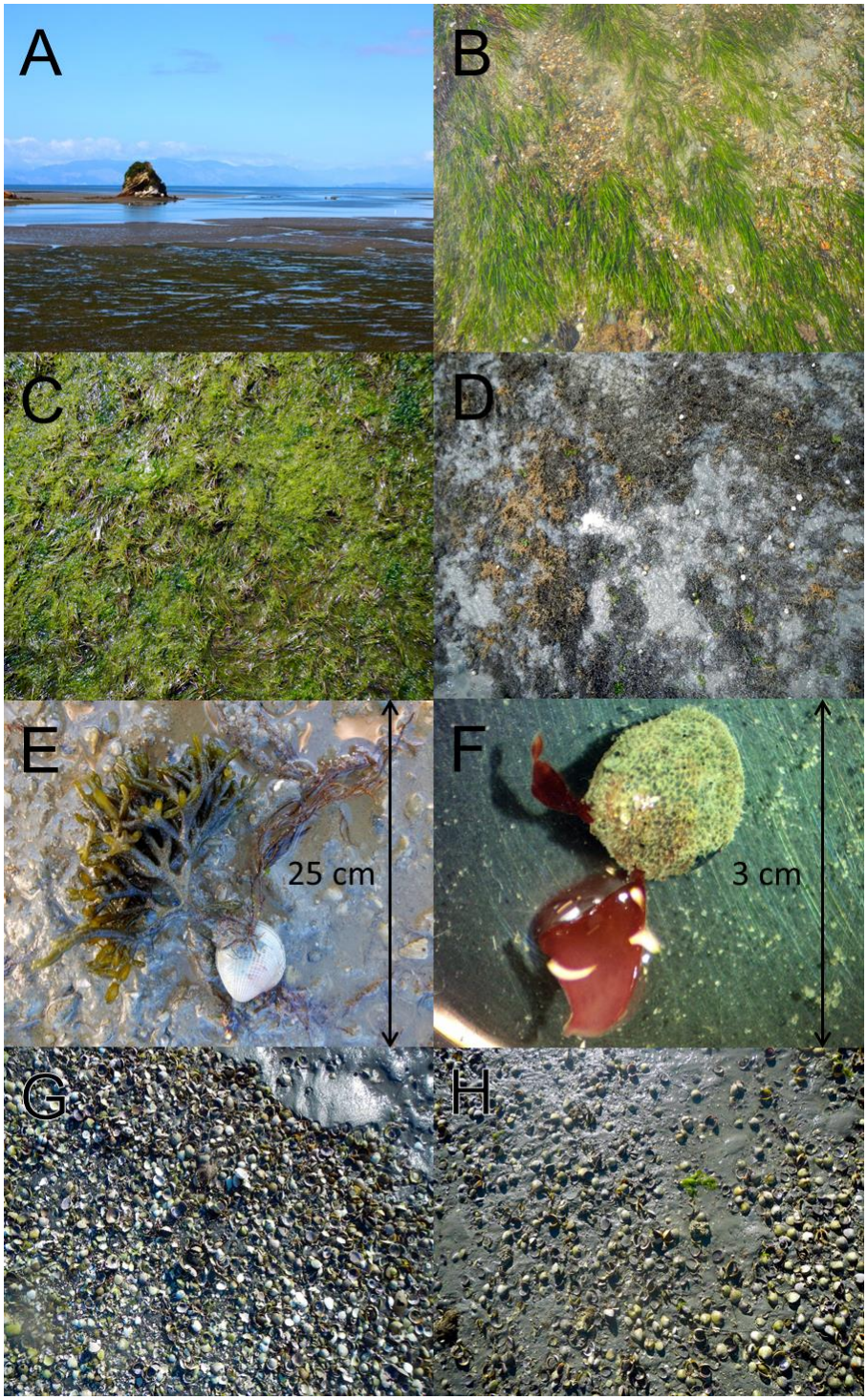
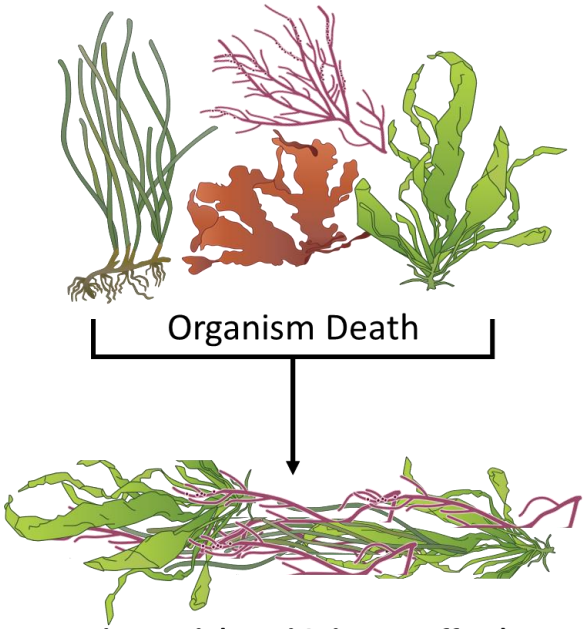
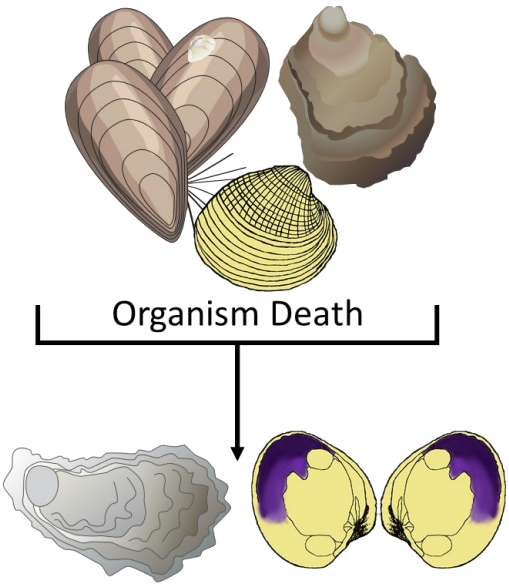


Figure 1.2 Examples of legacy effects of marine seagrass, seaweeds, and bivalves. Graphics used are from Integration and Application Network, University of Maryland Center for Environmental Science, as well as by the author.



Beach Wrack (Trophic legacy effect)

- Food for invertebrates
- Birds, spiders feed on invertebrates
- Nutrient cycling from decomposition



Dead Shells (Structural legacy effect)

- Shells persist in/on sediments
- Create habitat for algae, invertebrates
- Act as carbon sink
- Critical part of marine carbonate cycle

Figure 1.3 Examples of positive (green arrows) and negative (red arrows) interactions between (A) seagrass and seaweeds, (B) seagrass and bivalves, and (C) seaweeds and bivalves. Graphics used are from Integration and Application Network, University of Maryland Center for Environmental Science.

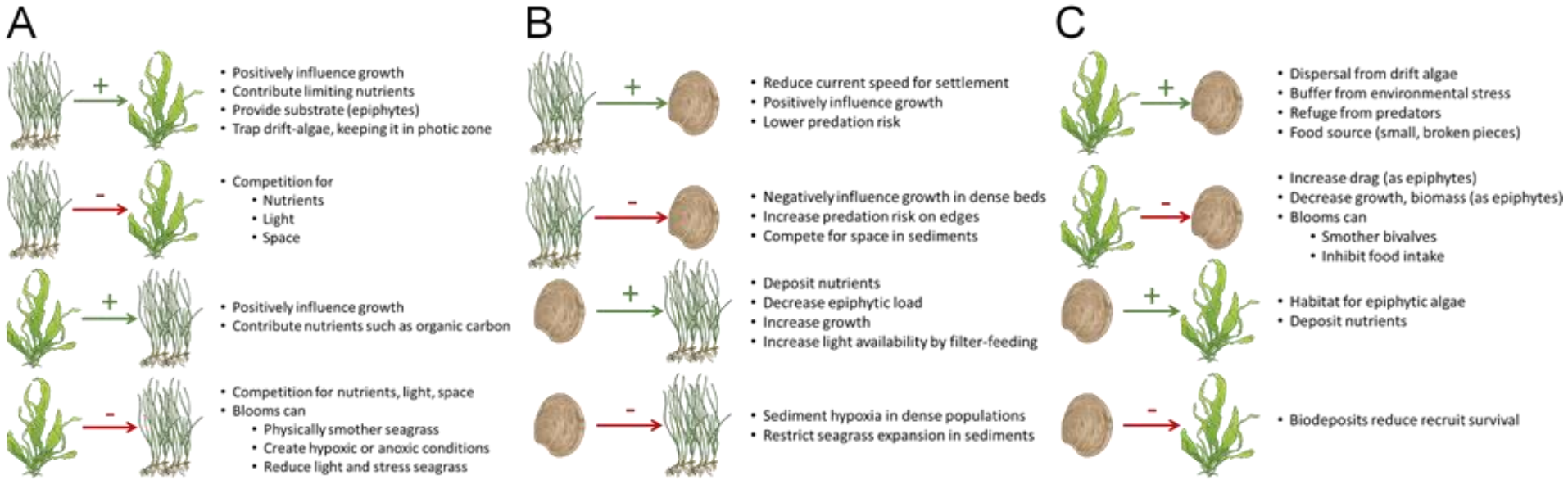
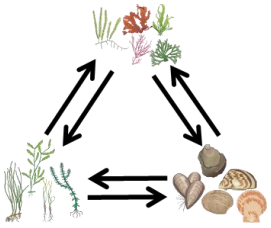


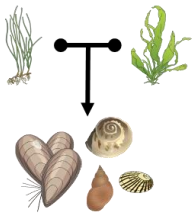
Figure 1.4 Locations of estuaries sampled in this thesis. (A) 16 estuaries from three latitudinal regions around the South Island of New Zealand, and (B) a detailed view of sampling locations within the Avon-Heathcote Estuary in Christchurch, New Zealand.

Figure 1.5 Graphical outline of themes from each data chapter in this thesis. Graphics used are from Integration and Application Network, University of Maryland Center for Environmental Science, as well as by the author.



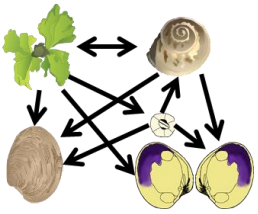
Chapter 2

Global interactions between angiosperms, seaweeds, and bivalves



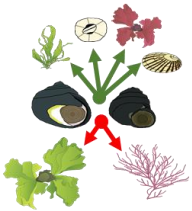
Chapter 3

Effects of seagrass and seaweeds on shell-forming species



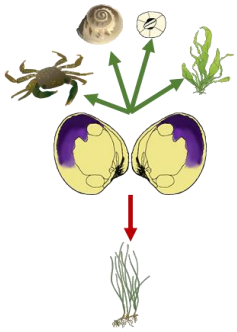
Chapter 4

Quantified interactions among biogenic habitat-forming taxa and habitat-users



Chapter 5

Top-down (grazing pressure) and bottom-up (habitat provision) impacts on benthic communities by two estuarine snails



Chapter 6

Effects of dead bivalve shells on benthic invertebrate and seaweed communities, and impacts on seagrass

References

Abbe, G. 1988. Population structure of the American oyster, *Crassostrea virginica,* on an oyster bar in central Chesapeake Bay: changes associated with shell planting and increased recruitment. Journal of Shellfish Research **7**:33-40.

Abbe, T. B., and D. R. Montgomery. 1996. Large woody debris jams, channel hydraulics, and habitat formation in large rivers. Regulated Rivers: Research & Management **12**:201-221.

Albrecht, A. S. 1998. Soft bottom versus hard rock: community ecology of macroalgae on intertidal mussel beds in the Wadden Sea. Journal of Experimental Marine Biology and Ecology **229**:85-109.

Allen, B. J., and S. L. Williams. 2003. Native eelgrass *Zostera marina* controls growth and reproduction of an invasive mussel through food limitation. Marine Ecology Progress Series **254**:57-67.

Altieri, A. H., B. R. Silliman, and M. D. Bertness. 2007. Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. The American Naturalist **169**:195-206.

Altieri, A. H., and J. D. Witman. 2006. Local extinction of a foundation species in a hypoxic estuary: integrating individuals to ecosystem. Ecology **87**:717-730.

Altieri, A. H., and J. D. Witman. 2014. Modular mobile foundation species as reservoirs of biodiversity. Ecosphere **5**:1-11.

Angelini, C., A. H. Altieri, B. R. Silliman, and M. D. Bertness. 2011. Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. BioScience **61**:782-789.

Auffrey, L. M., S. M. Robinson, and M. A. Barbeau. 2004. Effect of green macroalgal mats on burial depth of soft-shelled clams *Mya arenaria*. Marine Ecology Progress Series **278**:193-203.

Ayres-Peres, L., and F. L. Mantelatto. 2010. Epibiont occurrence on gastropod shells used by the hermit crab *Loxopagurus loxochelis* (Anomura: Diogenidae) on the northern coast of São Paulo, Brazil. Zoologia (Curitiba) **27**:222-227.

Bak, R. P. M. 1976. The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. Netherlands Journal of Sea Research **10**:285-337.

Battley, P. F., D. S. Melville, R. Schuckard, and P. F. Ballance. 2011. *Zostera muelleri* as a structuring agent of benthic communities in a large intertidal sandflat in New Zealand. Journal of Sea Research **65**:19-27.

Beal, B. 1994. Effects of seagrass (*Zostera marina*) cover on growth and survival of softshell clams (*Mya arenaria*). Journal of Shellfish Research **13**:311-312.

Beck, M. W., K. L. Heck Jr, K. W. Able, D. L. Childers, D. B. Eggleston, B. M. Gillanders, B. Halpern, C. G. Hays, K. Hoshino, and T. J. Minello. 2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates: A better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. BioScience **51**:633-641.

Bertness, M. D. 1984. Ribbed mussels and *Spartina alterniflora* production in a New England salt marsh. Ecology **65**:1794-1807.

Bertness, M. D., and G. H. Leonard. 1997. The role of positive interactions in communities: lessons from intertidal habitats. Ecology **78**:1976-1989.

Bertness, M. D., G. H. Leonard, J. M. Levine, P. R. Schmidt, and A. O. Ingraham. 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. Ecology **80**:2711-2726.

Beukema, J. 1982. Calcimass and carbonate production by molluscs on the tidal flats in the Dutch Wadden Sea: II The edible cockle, *Cerastoderma edule*. Netherlands Journal of Sea Research **15**:391-405.

Bishop, M. J., J. Fraser, and P. E. Gribben. 2013. Morphological traits and density of foundation species modulate a facilitation cascade in Australian mangroves. Ecology **94**:1927-1936.
Black, R., and C. Peterson. 1987. Biological vs. physical explanations for the non-random pattern of host occupation by a macroalga attaching to infaunal bivalve molluscs. Oecologia **73**:213-221.
Bologna, P. A., and K. L. Heck. 2000. Impacts of seagrass habitat architecture on bivalve settlement. Estuaries **23**:449-457.
Bologna, P. A. X., M. L. Fetzer, S. McDonnell, and E. M. Moody. 2005. Assessing the potential benthic–pelagic coupling in episodic blue mussel (*Mytilus edulis*) settlement events within eelgrass (*Zostera marina*) communities. Journal of Experimental Marine Biology and Ecology **316**:117-131.
Bologna, P. A. X., and K. L. Heck Jr. 1999. Macrofaunal associations with seagrass epiphytes relative importance of trophic and structural characteristics. Journal of Experimental Marine Biology and Ecology **242**:21-39.
Bolton-Ritchie, L., and M. Main. 2005. Nutrient water quality Avon-Heathcote Estuary/Ihutai, inputs, concentrations and potential effects. Environment Canterbury, Christchurch.
Borthagaray, A. I., and A. Carranza. 2007. Mussels as ecosystem engineers: Their contribution to species richness in a rocky littoral community. Acta Oecologica **31**:243-250.
Boström, C., E. L. Jackson, and C. A. Simenstad. 2006. Seagrass landscapes and their effects on associated fauna: A review. Estuarine, Coastal and Shelf Science **68**:383-403.
Box, A., A. Sureda, and S. Deudero. 2009. Antioxidant response of the bivalve *Pinna nobilis* colonised by invasive red macroalgae *Lophocladia lallemandii*. Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology **149**:456-460.
Brun, F. G., I. Hernández, J. J. Vergara, and J. L. Pérez-Lloréns. 2003a. Growth, carbon allocation and proteolytic activity in the seagrass *Zostera noltii* shaded by *Ulva* canopies. Functional Plant Biology **30**:551-560.
Brun, F. G., J. J. Vergara, G. Navarro, I. Hernández, and J. L. Pérez-Lloréns. 2003b. Effect of shading by *Ulva rigida* canopies on growth and carbon balance of the seagrass *Zostera noltii*. Marine Ecology Progress Series **265**:85-96.
Bunnell, F. L., I. Houde, B. Johnston, and E. Wind. 2002. How dead trees sustain live organisms in western forests. PSW-GTR-181.
Burkepile, D. E., and M. E. Hay. 2008. Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. Proceedings of the National Academy of Sciences **105**:16201-16206.
Buschbaum, C., and K. Reise. 1999. Effects of barnacle epibionts on the periwinkle *Littorina littorea* (L.). Helgoland Marine Research **53**:56-61.
Buschbaum, C., and B. Saier. 2001. Growth of the mussel *Mytilus edulis* L. in the Wadden Sea affected by tidal emergence and barnacle epibionts. Journal of Sea Research **45**:27-36.
Byers, J. E., P. E. Gribben, C. Yeager, and E. E. Sotka. 2012. Impacts of an abundant introduced ecosystem engineer within mudflats of the southeastern US coast. Biological Invasions **14**:2587-2600.
Cardoso, P., M. Pardal, D. Raffaelli, A. Baeta, and J. Marques. 2004. Macroinvertebrate response to different species of macroalgal mats and the role of disturbance history. Journal of Experimental Marine Biology and Ecology **308**:207-220.
Carlton, J. M. 1974. Land-building and Stabilization by Mangroves. Environmental Conservation **1**:285-294.
Ceccherelli, G., and F. Cinelli. 1998. Habitat effect on spatio-temporal variability in size and density of the introduced alga *Caulerpa taxifolia*. Marine Ecology Progress Series **163**:289-294.
Ceccherelli, G., and F. Cinelli. 1999. Effects of *Posidonia oceanica* canopy on *Caulerpa taxifolia* size in a north-western Mediterranean bay. Journal of Experimental Marine Biology and Ecology **240**:19-36.

Chan, D. H., and B. K. Chan. 2005. Effect of epibiosis on the fitness of the sandy shore snail *Batillaria zonalis* in Hong Kong. Marine Biology **146**:695-705.
Chapman, A. S., and R. L. Fletcher. 2002. Differential effects of sediments on survival and growth of *Fucus serratus* embryos (Fucales, Phaeophyceae). Journal of Phycology **38**:894-903.
Coen, L. D., R. D. Brumbaugh, D. Bushek, R. Grizzle, M. W. Luckenbach, M. H. Posey, S. P. Powers, and S. Tolley. 2007. Ecosystem services related to oyster restoration. Marine Ecology Progress Series **341**:303-307.
Coen, L. D., and K. L. Heck Jr. 1991. The interacting effects of siphon nipping and habitat on bivalve (*Mercenaria mercenaria* (L.)) growth in a subtropical seagrass (*Halodule wrightii* Aschers) meadow. Journal of Experimental Marine Biology and Ecology **145**:1-13.
Coen, L. D., and M. W. Luckenbach. 2000. Developing success criteria and goals for evaluating oyster reef restoration: Ecological function or resource exploitation? Ecological Engineering **15**:323-343.
Colombini, I., and L. Chellazi. 2003. Influence of marine allochthonous input on sandy beach communities. Oceanography and Marine Biology **41**:115.
Connolly, R. M., and J. S. Hindell. 2006. Review of nekton patterns and ecological processes in seagrass landscapes. Estuarine, Coastal and Shelf Science **68**:433-444.
Cooper, L. W., and C. P. McRoy. 1988. Anatomical adaptations to rocky substrates and surf exposure by the seagrass genus *Phyllospadix*. Aquatic Botany **32**:365-381.
Costanza, R., R. de Groot, P. Sutton, S. van der Ploeg, S. J. Anderson, I. Kubiszewski, S. Farber, and R. K. Turner. 2014. Changes in the global value of ecosystem services. Global Environmental Change **26**:152-158.
Croce, M. E., and E. R. Parodi. 2012. Seasonal dynamic of macroalgae in intertidal pools formed by beds of *Crassostrea gigas* (Mollusca, Bivalvia) on the north Patagonian Atlantic coast. Botanica Marina **55**:49-58.
Cuddington, K. 2011. Legacy Effects: The persistent impact of ecological interactions. Biological Theory **6**:203-210.
Cummins, S., D. Roberts, and K. Zimmerman. 2004. Effects of the green macroalga *Enteromorpha intestinalis* on macrobenthic and seagrass assemblages in a shallow coastal estuary. Marine Ecology Progress Series **266**:77-87.
Dame, R., T. Wolaver, and S. Libes. 1985. The summer uptake and release of nitrogen by an intertidal oyster reef. Netherlands Journal of Sea Research **19**:265-268.
Dame, R., R. Zingmark, H. Stevenson, and D. Nelson. 1980. Filter feeder coupling between the estuarine water column and benthic subsystems. Pages 521-526 *in* Estuarine Perspectives. Academic Press, New York.
Dame, R. F., J. D. Spurrier, and T. G. Wolaver. 1989. Carbon, nitrogen and phosphorus processing by an oyster reef. Marine Ecology Progress Series **54**:249-256.
Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. Pages 81-96 *in* Proceedings of the colloquium on conservation problems in Antarctica. Allen Press Lawrence, Kansas, USA.
Dayton, P. K. 1973. Dispersion, dispersal, and persistence of the annual intertidal alga, *Postelsia palmaeformis* Ruprecht. Ecology **54**:433-438.
den Hartog, C. 1970. The seagrasses of the world. North Holland Publishing Co., Amsterdam.
Diaz, M. C., and K. Rützler. 2001. Sponges: an essential component of Caribbean coral reefs. Bulletin of Marine Science **69**:535-546.
Dijkstra, J. A., J. Boudreau, and M. Dionne. 2012. Species-specific mediation of temperature and community interactions by multiple foundation species. Oikos **121**:646-654.
Dittman, D., and C. Robles. 1991. Effect of algal epiphytes on the mussel *Mytilus Californianus*. Ecology **72**:286-296.
Dodson, S. I. 1970. Complementary feeding niches sustained by size-selective predation. Limnology and Oceanography **15**:131-137.

Donadi, S., T. van der Heide, T. Piersma, E. M. van der Zee, E. J. Weerman, J. van de Koppel, H. Olff, C. Devine, U. E. Hernawan, M. Boers, L. Planthof, and B. Klemens Eriksson. 2015. Multi-scale habitat modification by coexisting ecosystem engineers drives spatial separation of macrobenthic functional groups. Oikos **124**:1502-1510.

Duarte, C. M., and C. L. Chiscano. 1999. Seagrass biomass and production: a reassessment. Aquatic Botany **65**:159-174.

Duarte, C. M., J. W. Fourqurean, D. Krause-Jensen, and B. Olesen. 2006. Dynamics of Seagrass Stability and Change. Pages 271-294 *in* A. W. D. Larkum, R. J. Orth, and C. M. Duarte, editors. Seagrasses: Biology, Ecology, and Conservation. Springer Netherlands, Dordrecht.

Dudgeon, S., and P. S. Petraitis. 2005. First year demography of the foundation species, *Ascophyllum nodosum*, and its community implications. Oikos **109**:405-415.

Dugan, J. E., D. M. Hubbard, M. D. McCrary, and M. O. Pierson. 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. Estuarine, Coastal and Shelf Science **58**:25-40.

Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, and G. M. Lovett. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment **3**:479-486.

Everett, R. A. 1991. Intertidal distribution of infauna in a central California lagoon: the role of seasonal blooms of macroalgae. Journal of Experimental Marine Biology and Ecology **150**:223-247.

Fonseca, M. S., and J. A. Cahalan. 1992. A preliminary evaluation of wave attenuation by four species of seagrass. Estuarine, Coastal and Shelf Science **35**:565-576.

Fourqurean, J. W., C. M. Duarte, H. Kennedy, N. Marba, M. Holmer, M. A. Mateo, E. T. Apostolaki, G. A. Kendrick, D. Krause-Jensen, and K. J. McGlathery. 2012. Seagrass ecosystems as a globally significant carbon stock. Nature Geoscience **5**:505.

Franklin, J. F., H. H. Shugart, and M. E. Harmon. 1987. Tree death as an ecological process. BioScience **37**:550-556.

Franssen, S. U., J. Gu, N. Bergmann, G. Winters, U. C. Klostermeier, P. Rosenstiel, E. Bornberg-Bauer, and T. B. H. Reusch. 2011. Transcriptomic resilience to global warming in the seagrass *Zostera marina*, a marine foundation species. Proceedings of the National Academy of Sciences **108**:19276-19281.

Gain, I. E., R. A. Brewton, M. M. Reese Robillard, K. D. Johnson, D. L. Smee, and G. W. Stunz. 2016. Macrofauna using intertidal oyster reef varies in relation to position within the estuarine habitat mosaic. Marine Biology **164**:8.

Geertz-Hansen, O., K. Sand-Jensen, D. F. Hansen, and A. Christiansen. 1993. Growth and grazing control of abundance of the marine macroalga, *Ulva lactuca* L. in a eutrophic Danish estuary. Aquatic Botany **46**:101-109.

Grabowski, J. H., and C. H. Peterson. 2007. Restoring oyster reefs to recover ecosystem services. Pages 281-298 *in* C. K, B. JE, W. W, and H. A, editors. Ecosystem engineers: plants to protists. Academic Press, New York, NY.

Gribben, P. E., J. E. Byers, M. Clements, L. A. McKenzie, P. D. Steinberg, and J. T. Wright. 2009. Behavioural interactions between ecosystem engineers control community species richness. Ecol Lett **12**:1127-1136.

Gribben, P. E., and J. T. Wright. 2006. Invasive seaweed enhances recruitment of a native bivalve: roles of refuge from predation and the habitat choice of recruits. Marine Ecology Progress Series **318**:177-185.

Grizzle, R. E., F. T. Short, C. R. Newell, H. Hoven, and L. Kindblom. 1996. Hydrodynamically induced synchronous waving of seagrasses:'monami'and its possible effects on larval mussel settlement. Journal of Experimental Marine Biology and Ecology **206**:165-177.

Gutiérrez, J. L., C. G. Jones, D. L. Strayer, and O. O. Iribarne. 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos **101**:79-90.
Gutt, J., and T. Schickan. 1998. Epibiotic relationships in the Antarctic benthos. Antarctic Science **10**:398-405.
Hall-Spencer, J., and P. Moore. 2000. *Limaria hians* (Mollusca: Limacea): a neglected reef-forming keystone species. Aquatic Conservation-Marine and Freshwater Ecosystems **10**.
Han, Q. Y., and D. Y. Liu. 2014. Macroalgae blooms and their effects on seagrass ecosystems. Journal of Ocean University of China **13**:791-798.
Hanke, M. H., M. H. Posey, and T. D. Alphin. 2017. The effects of intertidal oyster reef habitat characteristics on faunal utilization. Marine Ecology Progress Series **581**:57-70.
Harlin, M. M. 1975. Epiphyte—host relations in seagrass communities. Aquatic Botany **1**:125-131.
Harlin, M. M., and B. Thorne-Miller. 1981. Nutrient enrichment of seagrass beds in a Rhode Island coastal lagoon. Marine Biology **65**:221-229.
Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research **15**:133-302.
Harrison, P. G., and K. H. Mann. 1975. Chemical changes during the seasonal cycle of growth and decay in eelgrass (*Zostera marina*) on the Atlantic Coast of Canada. Journal of the Fisheries Research Board of Canada **32**:615-621.
Hastings, A., J. E. Byers, J. A. Crooks, K. Cuddington, C. G. Jones, J. G. Lambrinos, T. S. Talley, and W. G. Wilson. 2007. Ecosystem engineering in space and time. Ecology Letters **10**:153-164.
Hauxwell, J., J. Cebrián, C. Furlong, and I. Valiela. 2001. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. Ecology **82**:1007-1022.
Henderson, J., and J. O'Neil. 2003. Economic values associated with construction of oyster reefs by the Corps of Engineers. Enginner Research and Development Center, Vicksburg, MS.
Hinchey, E. K., L. C. Schaffner, C. C. Hoar, B. W. Vogt, and L. P. Batte. 2006. Responses of estuarine benthic invertebrates to sediment burial: the importance of mobility and adaptation. Hydrobiologia **556**:85-98.
Hollever, J., and L. Bolton-Ritchie. 2016. Broad scale mapping of the Estuary of the Heathcote and Avon Rivers/Ihutai. Environment Canterbury.
Holmquist, J. 1994. Benthic macroalgae as a dispersal mechanism for fauna: influence of a marine tumbleweed. Journal of Experimental Marine Biology and Ecology **180**:235-251.
Hondula, K. L., and M. L. Pace. 2014. Macroalgal support of cultured hard clams in a low nitrogen coastal lagoon. Marine Ecology Progress Series **498**:187-201.
Hughes, A. R., S. L. Williams, C. M. Duarte, K. L. Heck Jr, and M. Waycott. 2008. Associations of concern: declining seagrasses and threatened dependent species. Frontiers in Ecology and the Environment **7**:242-246.
Ingólfsson, A. 1995. Floating clumps of seaweed around Iceland: natural microcosms and a means of dispersal for shore fauna. Marine Biology **122**:13-21.
Irlandi, E. 1994. Large-and small-scale effects of habitat structure on rates of predation: how percent coverage of seagrass affects rates of predation and siphon nipping on an infaunal bivalve. Oecologia **98**:176-183.
Irlandi, E. 1996. The effects of seagrass patch size and energy regime on growth of a suspension-feeding bivalve. Journal of Marine Research **54**:161-185.
Irlandi, E. A. 1997. Seagrass patch size and survivorship of an infaunal bivalve. Oikos **78**:511-518.
Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos **69**:373-386.
Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology **78**:1946-1957.

Jones, M., and E. Pinn. 2006. The impact of a macroalgal mat on benthic biodiversity in Poole Harbour. Marine Pollution Bulletin **53**:63-71.

Jones, M. B., and M. J. Simons. 1982. Habitat preferences of two estuarine burrowing crabs *Helice crassa* Dana (Grapsidae) and *Macrophtalmus hirtipes* (Jacquinot) (Ocypodidae). Journal of Experimental Marine Biology and Ecology **56**:49-62.

Judge, M. L., L. D. Coen, and K. L. Heck Jr. 1993. Does *Mercenaria mercenaria* encounter elevated food levels in seagrass beds? Results from a novel technique to collect suspended food resources. Marine Ecology Progress Series **92**:141-150.

Jupp, K., T. Partridge, D. Hart, and I. Marsden. 2007. Ecology of the Avon-Heathcote Estuary: Comparative Salt Marsh Survey 2006-2007. Estuarine Research Report 34. University of Canterbury. School of Biological Sciences.

Kang, C., P. Sauriau, P. Richard, and G. Blanchard. 1999. Food sources of the infaunal suspension-feeding bivalve *Cerastoderma edule* in a muddy sandflat of Marennes-Oléron Bay, as determined by analyses of carbon and nitrogen stable isotopes. Marine Ecology Progress Series **187**:147-158.

Kappelle, M., J.-G. Van Uffelen, and A. M. Cleef. 1995. Altitudinal zonation of montane *Quercus* forests along two transects in Chirripó National Park, Costa Rica. Vegetatio **119**:119-153.

Khailov, K., and Z. Burlakova. 1969. Release of dissolved organic matter by marine seaweeds and distribution of their total organic production to inshore communities. Limnology and Oceanography **14**:521-527.

Kidwell, S. M. 1986. Taphonomic feedback in miocene assemblages: testing the role of dead hardparts in benthic communities. Palaios **1**:239-255.

Kidwell, S. M., and D. Jablonski. 1983. Taphonomic feedback: ecological consequences of shell accumulation. Pages 195-248 *in* M. J. S. Tevesz and P. L. McCall, editors. Biotic Interactions in Recent and Fossil Benthic Communities. Springer US, Boston, MA.

Knox, G. A., A. R. Kilner, and C. D. Board. 1973. The ecology of the Avon-Heathcote estuary. Estuarine Research Unit, Department of Zoology, University of Canterbury [for] Christchurch Drainage Board.

Kotta, J., K. Herkül, I. Kotta, H. Orav-Kotta, and V. Lauringson. 2009. Effects of the suspension feeding mussel *Mytilus trossulus* on a brackish water macroalgal and associated invertebrate community. Marine Ecology **30**:56-64.

Kuo, J., and C. den Hartog. 2006. Seagrass morphology, anatomy, and ultrastructure. Pages 51-87 *in* A. W. D. Larkum, R. J. Orth, and C. M. Duarte, editors. Seagrasses: Biology, Ecology, and Conservation. Springer Netherlands, Dordrecht.

Lehnert, R. L., and D. M. Allen. 2002. Nekton use of subtidal oyster shell habitat in a Southeastern U.S. estuary. Estuaries **25**:1015-1024.

Leuschner, C., H. F. Jungkunst, and S. Fleck. 2009. Functional role of forest diversity: pros and cons of synthetic stands and across-site comparisons in established forests. Basic and Applied Ecology **10**:1-9.

Lilley, S. A., and D. R. Schiel. 2006. Community effects following the deletion of a habitat-forming alga from rocky marine shores. Oecologia **148**:672-681.

Linse, K., L. J. Walker, and D. K. Barnes. 2008. Biodiversity of echinoids and their epibionts around the Scotia Arc, Antarctica. Antarctic Science **20**:227-244.

Lobelle, D., E. J. Kenyon, K. J. Cook, and J. C. Bull. 2013. Local competition and metapopulation processes drive long-term seagrass-epiphyte population dynamics. PLoS One **8**:e57072.

López, M. S., and R. Coutinho. 2010. Positive interaction between the native macroalgae *Sargassum* sp. and the exotic bivalve *Isognomon bicolor*? Brazilian Journal of Oceanography **58**:69-72.

Lubchenco, J., and B. A. Menge. 1978. Community development and persistence in a low rocky intertidal zone. Ecological Monographs **48**:67-94.

Lyons, D. A., C. Arvanitidis, A. J. Blight, E. Chatzinikolaou, T. Guy-Haim, J. Kotta, H. Orav-Kotta, A. M. Queirós, G. Rilov, and P. J. Somerfield. 2014. Macroalgal blooms alter community structure and primary productivity in marine ecosystems. Global Change Biology **20**:2712-2724.

MacIsaac, H. J. 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. American Zoologist **36**:287-299.

Marbà, N., M. Holmer, E. Gacia, and C. Barron. 2006. Seagrass beds and coastal biogeochemistry. Pages 135-157 *in* A. W. D. Larkum, R. J. Orth, and C. M. Duarte, editors. Seagrasses: biology, ecology and conservation. Springer Netherlands, Dordrecht.

Marsden, I. D. 2004. Effects of reduced salinity and seston availability on growth of the New Zealand little-neck clam *Austrovenus stutchburyi*. Marine Ecology Progress Series **266**:157-171.

Marsden, I. D., and N. Baharuddin. 2015. Gastropod growth and survival as bioindicators of stress associated with high nutrients in the intertidal of a shallow temperate estuary. Estuarine, Coastal and Shelf Science **156**:175-185.

Marsden, I. D., and M. J. Bressington. 2009. Effects of macroalgal mats and hypoxia on burrowing depth of the New Zealand cockle (*Austrovenus stutchburyi*). Estuarine, Coastal and Shelf Science **81**:438-444.

Marsden, I. D., B. D. Smith, and P. S. Rainbow. 2014. Effects of environmental and physiological variables on the accumulated concentrations of trace metals in the New Zealand cockle *Austrovenus stutchburyi*. Science of the Total Environment **470-471**:324-339.

Maser, C., R. G. Anderson, K. Cromack Jr, J. T. Williams, and R. E. Martin. 1979. Dead and down woody material. Pages 78-95 *in* J. W. Thomas, editor. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. U.S. Department of Agriculture, U.S. Forestry Service, Portland, OR.

McClatchie, S., S. K. Juniper, and G. A. Knox. 1982. Structure of a mudflat diatom community in the Avon-Heathcote Estuary, New Zealand. New Zealand Journal of Marine and Freshwater Research **16**:299-309.

McGlathery, K. J. 2001. Macroalgal blooms contribute to the decline of seagrass in nutrient-enriched waters. Journal of Phycology **37**:453-456.

Measures, R., M. Hicks, U. Shankar, J. Bind, J. Arnold, and J. Zeldis. 2011. Mapping earthquake induced topographical change and liquefaction in the Avon-Heathcote Estuary.

Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecological Monographs **46**:355-393.

Mills, L. S., M. E. Soulé, and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. BioScience **43**:219-224.

Mistri, M., R. Rossi, and E. Fano. 2004. The spread of an alien bivalve (*Musculista senhousia*) in the Sacca di Goro Lagoon (Adriatic Sea, Italy). Journal of Molluscan Studies **70**:257-261.

Molina, R., and M. Amaranthus. 1991. Rhizosphere biology: ecological linkages between soil processes, plant growth, and community dynamics. United States Forest Service, Boise, ID.

Mtolera, M. S. 2003. Effect of seagrass cover and mineral content on *Kappaphycus* and *Eucheuma* productivity in Zanzibar. Western Indian Ocean Journal of Marine Science **2**:163-170.

Munari, C., N. Bocchi, and M. Mistri. 2015. Epifauna associated to the introduced *Gracilaria vermiculophylla* (Rhodophyta; Florideophyceae: Gracilariales) and comparison with the native *Ulva rigida* (Chlorophyta; Ulvophyceae: Ulvales) in an Adriatic lagoon. Italian Journal of Zoology **82**:436-445.

Mvungi, E. F. 2011. Seagrasses and Eutrophication - Interactions between seagrass photosynthesis, epiphytes, macroalgae and mussels. Doctoral thesis. Stockholm University.

Mvungi, E. F., T. J. Lyimo, and M. Björk. 2012. When *Zostera marina* is intermixed with *Ulva*, its photosynthesis is reduced by increased pH and lower light, but not by changes in light quality. Aquatic Botany **102**:44-49.

Nadkarni, N. M. 1994. Diversity of species and interactions in the upper tree canopy of forest ecosystems. American Zoologist **34**:70-78.

Nadrowski, K., C. Wirth, and M. Scherer-Lorenzen. 2010. Is forest diversity driving ecosystem function and service? Current Opinion in Environmental Sustainability **2**:75-79.
Nagelkerken, I., G. van der Velde, M. W. Gorissen, G. J. Meijer, T. Van't Hof, and C. den Hartog. 2000. Importance of mangroves, seagrass Beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Estuarine, Coastal and Shelf Science **51**:31-44.
Nakaoka, M. 2005. Plant–animal interactions in seagrass beds: ongoing and future challenges for understanding population and community dynamics. Population Ecology **47**:167-177.
Nebelsick, J. H., B. Schmid, and M. Stachowitsch. 1997. The encrustation of fossil and recent sea-urchin tests: ecological and taphonomic significance. Lethaia **30**:271-284.
Nelson, T. A., and A. Lee. 2001. A manipulative experiment demonstrates that blooms of the macroalga *Ulvaria obscura* can reduce eelgrass shoot density. Aquatic Botany **71**:149-154.
Newell, R. I. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. Journal of Shellfish Research **23**:51-62.
Newell, R. I., and E. W. Koch. 2004. Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. Estuaries **27**:793-806.
Norkko, J., E. Bonsdorff, and A. Norkko. 2000. Drifting algal mats as an alternative habitat for benthic invertebrates: Species specific responses to a transient resource. Journal of Experimental Marine Biology and Ecology **248**:79-104.
Norling, P., and N. Kautsky. 2007. Structural and functional effects of *Mytilus edulis* on diversity of associated species and ecosystem functioning. Marine Ecology Progress Series **351**:163.
O'Connor, N. E., T. P. Crowe, and D. McGrath. 2006. Effects of epibiotic algae on the survival, biomass and recruitment of mussels, *Mytilus* L. (Bivalvia: Mollusca). Journal of Experimental Marine Biology and Ecology **328**:265-276.
Olabarria, C., M. Incera, J. Garrido, and F. Rossi. 2010. The effect of wrack composition and diversity on macrofaunal assemblages in intertidal marine sediments. Journal of Experimental Marine Biology and Ecology **396**:18-26.
Olesen, B., N. Marbà, C. M. Duarte, R. S. Savela, and M. D. Fortes. 2004. Recolonization dynamics in a mixed seagrass meadow: the role of clonal versus sexual processes. Estuaries **27**:770-780.
Orth, R. J. 1977. The importance of sediment stability in seagrass communities. Pages 281-300 *in* B. C. Coull, editor. Ecology of Marine Benthos. University of South Carolina Press, Columbia.
Orth, R. J., T. J. Carruthers, W. C. Dennison, C. M. Duarte, J. W. Fourqurean, K. L. Heck, A. R. Hughes, G. A. Kendrick, W. J. Kenworthy, and S. Olyarnik. 2006. A global crisis for seagrass ecosystems. BioScience **56**:987-996.
Orth, R. J., and J. Van Montfrans. 1984. Epiphyte-seagrass relationships with an emphasis on the role of micrograzing: a review. Aquatic Botany **18**:43-69.
Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. Limnology and Oceanography **14**:710-719.
Palmer, T. J., P. D. Taylor, and J. A. Todd. 1993. Epibiont shadowing: a hitherto unrecognized way of preserving soft-bodied fossils. Terra Nova **5**:568-572.
Pavia, H., H. Carr, and P. Åberg. 1999. Habitat and feeding preferences of crustacean mesoherbivores inhabiting the brown seaweed *Ascophyllum nodosum* (L.) Le Jol. and its epiphytic macroalgae. Journal of Experimental Marine Biology and Ecology **236**:15-32.
Peake, A. J., and G. P. Quinn. 1993. Temporal variation in species-area curves for invertebrates in clumps of an intertidal mussel. Ecography **16**:269-277.
Peterson, B. J., and K. L. Heck Jr. 1999. The potential for suspension feeding bivalves to increase seagrass productivity. Journal of Experimental Marine Biology and Ecology **240**:37-52.
Peterson, B. J., and K. L. Heck Jr. 2001a. An experimental test of the mechanism by which suspension feeding bivalves elevate seagrass productivity. Marine Ecology Progress Series **218**:115-125.

Peterson, B. J., and K. L. Heck Jr. 2001b. Positive interactions between suspension-feeding bivalves and seagrass-a facultative mutualism. Marine Ecology Progress Series **213**:143-155.

Peterson, C. H., H. Summerson, and P. Duncan. 1984. The influence of seagrass cover on population structure and individual growth rate of a suspension-feeding bivalve, *Mercenaria mercenaria*. Journal of Marine Research **42**:123-138.

Phillippi, A., K. Tran, and A. Perna. 2014. Does intertidal canopy removal of *Ascophyllum nodosum* alter the community structure beneath? Journal of Experimental Marine Biology and Ecology **461**:53-60.

Posey, M. H., T. D. Alphin, C. M. Powell, and E. Townsend. 1999. Use of oyster reefs as habitat for epibenthic fish and decapods. Pages 229-237 *in* Luckenbach, M., Mann, R., Wesson, J. editors. Oyster reef habitat restoration: a synopsis and synthesis of approaches. Virginia Institute of Marine Science Press, Williamsburg, PA.

Powell, E. N., J. N. Kraeuter, and K. A. Ashton-Alcox. 2006. How long does oyster shell last on an oyster reef? Estuarine, Coastal and Shelf Science **69**:531-542.

Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, G. Daily, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. BioScience:609-620.

Powers, M. J., C. H. Peterson, H. C. Summerson, and S. P. Powers. 2007. Macroalgal growth on bivalve aquaculture netting enhances nursery habitat for mobile invertebrates and juvenile fishes. Marine Ecology Progress Series **339**:109-122.

Purchase, N. G., and J. E. Fergusson. 1986. The distribution and geochemistry of lead in river sediments, Christchurch, New Zealand. Environmental Pollution Series B, Chemical and Physical **12**:203-216.

Raffaelli, D. G., J. A. Raven, and L. J. Poole. 1998. Ecological impact of green macroalgal blooms. Oceanography and Marine Biology: an annual review **36**:97-125.

Rainer, S. F., and V. A. Wadley. 1991. Abundance, growth and production of the bivalve *Solemya* sp., a food source for juvenile rock lobsters in a seagrass community in Western Australia. Journal of Experimental Marine Biology and Ecology **152**:201-223.

Ramus, A. P., B. R. Silliman, M. S. Thomsen, and Z. T. Long. 2017. An invasive foundation species enhances multifunctionality in a coastal ecosystem. Proceedings of the National Academy of Sciences **114**:8580-8585.

Rasheed, M. A. 2004. Recovery and succession in a multi-species tropical seagrass meadow following experimental disturbance: the role of sexual and asexual reproduction. Journal of Experimental Marine Biology and Ecology **310**:13-45.

Reusch, T., A. Chapman, and J. Groger. 1994. Blue mussels *Mytilus edulis* do not interfere with eelgrass *Zostera marina* but fertilize shoot growth through biodeposition. Marine Ecology Progress Series **108**:265-282.

Reusch, T. B., and S. L. Williams. 1998. Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia*. Oecologia **113**:428-441.

Reusch, T. B. H., and A. R. O. Chapman. 1995. Storm effects on eelgrass (*Zostera marina* L.) and blue mussel (*Mytilus edulis* L.) beds. Journal of Experimental Marine Biology and Ecology **192**:257-271.

Ricciardi, A., F. G. Whoriskey, and J. B. Rasmussen. 1997. The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. Canadian Journal of Fisheries and Aquatic Sciences **54**:2596-2608.

Rodil, I. F., C. Olabarria, M. Lastra, and J. López. 2008. Differential effects of native and invasive algal wrack on macrofaunal assemblages inhabiting exposed sandy beaches. Journal of Experimental Marine Biology and Ecology **358**:1-13.

Rodrigo, A. G. 1989. Surficial sediment-heavy metal associations in the Avon-Heathcote Estuary, New Zealand. New Zealand Journal of Marine and Freshwater Research **23**:255-262.

Roper, D. S., M. J. Simons, and M. B. Jones. 1983. Distribution of zooplankton in the Avon-Heathcote Estuary, Christchurch. New Zealand Journal of Marine and Freshwater Research **17**:267-278.

Sammarco, P. W. 1982. Effects of grazing by *Diadema antillarum* Philippi (Echinodermata: Echinoidea) on algal diversity and community structure. Journal of Experimental Marine Biology and Ecology **65**:83-105.

Sandford, F. 2003. Population dynamics and epibiont associations of hermit crabs (Crustacea: Decapoda: Paguroidea) on Dog Island, Florida. Memoirs of Museum Victoria **60**:45-52.

Saunders, J. E., M. J. Attrill, S. M. Shaw, and A. A. Rowden. 2003. Spatial variability in the epiphytic algal assemblages of *Zostera marina* seagrass beds. Marine Ecology Progress Series **249**:107-115.

Schejter, L., and C. Bremec. 2007. Benthic richness in the Argentine continental shelf: the role of *Zygochlamys patagonica* (Mollusca: Bivalvia: Pectinidae) as settlement substrate. Journal of the Marine Biological Association of the United Kingdom **87**:917-925.

Schiel, D. R. 2006. Rivets or bolts? When single species count in the function of temperate rocky reef communities. Journal of Experimental Marine Biology and Ecology **338**:233-252.

Schiel, D. R., and S. A. Lilley. 2011. Impacts and negative feedbacks in community recovery over eight years following removal of habitat-forming macroalgae. Journal of Experimental Marine Biology and Ecology **407**:108-115.

Schmidt, A. L., M. Coll, T. N. Romanuk, and H. K. Lotze. 2011. Ecosystem structure and services in eelgrass *Zostera marina* and rockweed *Ascophyllum nodosum* habitats. Marine Ecology Progress Series **437**:51-68.

Schneider, C. L. 2003. Hitchhiking on Pennsylvanian echinoids: epibionts on *Archaeocidaris*. Palaios **18**:435-444.

Schuhmacher, H. 1977. Initial phases in reef development, studied at artificial reef types off Eilat, (Red Sea). Helgoländer wissenschaftliche Meeresuntersuchungen **30**:400-411.

Sedell, J. R., and J. L. Froggatt. 1984. Importance of streamside forests to large rivers: the isolation of the Willamette River, Oregon, USA, from its floodplain by snagging and streamside forest removal. Internationale Vereinigung fur Theoretische und Angewandte Limnologie **22**:1828-1834.

Skilton, J. E. 2013. Invertebrate responses to large-scale change: impacts of euthrophication and cataclysmic earthquake events in a southern New Zealand estuary. PhD Thesis. University of Canterbury, Christchurch, New Zealand.

Smith, T. J. and N. C. Duke. 1983. Physical determinants of inter-estuary variation in mangrove species richness around the tropical coastline of Australia. Journal of Biogeography **14**:9-19.

Smith, K. A., E. W. North, F. Shi, S.-N. Chen, R. R. Hood, E. W. Koch, and R. I. Newell. 2009. Modeling the effects of oyster reefs and breakwaters on seagrass growth. Estuaries and Coasts **32**:748-757.

Sousa, W. P. 1984. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. Ecology **65**:1918-1935.

Sousa, W. P., P. G. Kennedy, B. J. Mitchell, and B. M. Ordóñez L. 2007. Supply-side ecology in mangroves: do propagule dispersal and seedling establishment explain forest structure?. Ecological Monographs **7**: 53-76.

Suchanek, T. H. 1992. Extreme biodiversity in the marine environment: mussel bed communities of *Mytilus californianus*. Northwest Environmental Journal **8**:150-152.

Sugimoto, K., K. Hiraoka, S. Ohta, Y. Niimura, T. Terawaki, and M. Okada. 2007. Effects of ulvoid (*Ulva* spp.) accumulation on the structure and function of eelgrass (*Zostera marina* L.) bed. Marine Pollution Bulletin **54**:1582-1585.

Thiel, M., L. Stearns, and L. Watling. 1998. Effects of green algal mats on bivalves in a New England mud flat. Helgoländer Meeresuntersuchungen **52**:15-28.

Thieltges, D. W., and C. Buschbaum. 2007. Vicious circle in the intertidal: facilitation between barnacle epibionts, a shell boring polychaete and trematode parasites in the periwinkle *Littorina littorea*. Journal of Experimental Marine Biology and Ecology **340**:90-95.

Thomsen, M., P. Stæhr, L. Nejrup, and D. Schiel. 2013. Effects of the invasive macroalgae *Gracilaria vermiculophylla* on two co-occurring foundation species and associated invertebrates. Aquatic Invasions **8**:133-145.

Thomsen, M. S., A. H. Altieri, C. Angelini, M. J. Bishop, P. E. Gribben, G. Lear, Q. He, D. R. Schiel, B. R. Silliman, P. M. South, D. M. Watson, T. Wernberg, and G. Zotz. 2018. Secondary foundation species enhance biodiversity. Nature Ecology & Evolution **2**:634-639.

Thomsen, M. S., T. Hildebrand, P. M. South, T. Foster, A. Siciliano, E. Oldach, and D. R. Schiel. 2016. A sixth-level habitat cascade increases biodiversity in an intertidal estuary. Ecology and evolution **6**:8291-8303.

Thomsen, M. S., K. McGlathery, A. Schwarzschild, and B. Silliman. 2009. Distribution and ecological role of the non-native macroalga *Gracilaria vermiculophylla* in Virginia salt marshes. Biological Invasions **11**:2303-2316.

Thomsen, M. S., and T. Wernberg. 2015. The devil in the detail: harmful seaweeds are not harmful to everyone. Global Change Biology **21**:1381-1382.

Thomsen, M. S., T. Wernberg, A. Altieri, F. Tuya, D. Gulbransen, K. J. McGlathery, M. Holmer, and B. R. Silliman. 2010a. Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. Integrative and Comparative Biology **50**:158-175.

Thomsen, M. S., T. Wernberg, F. Tuya, and B. R. Silliman. 2010b. Ecological performance and possible origin of a ubiquitous but under-studied gastropod. Estuarine, Coastal and Shelf Science **87**:501-509.

Thomson, J. A., D. A. Burkholder, M. R. Heithaus, J. W. Fourqurean, M. W. Fraser, J. Statton, and G. A. Kendrick. 2015. Extreme temperatures, foundation species, and abrupt ecosystem change: an example from an iconic seagrass ecosystem. Global Change Biology **21**:1463-1474.

Thrush, S. F., J. E. Hewitt, A. Norkko, P. E. Nicholls, G. E. Funnell, and J. I. Ellis. 2003. Habitat change in estuaries: predicting broad-scale responses of intertidal macrofauna to sediment mud content. Marine Ecology Progress Series **263**:101-112.

Thyrring, J., M. S. Thomsen, and T. Wernberg. 2013. Large-scale facilitation of a sessile community by an invasive habitat-forming snail. Helgoland Marine Research **67**:789-794.

Turner, T. 1985. Stability of rocky intertidal surfgrass beds: persistence, preempton, and recovery. Ecology **66**:83-92.

Tuya, F., M. A. Vanderklift, G. A. Hyndes, T. Wernberg, M. S. Thomsen, and C. Hanson. 2010. Proximity to rocky reefs alters the balance between positive and negative effects on seagrass fauna. Marine Ecology Progress Series **405**:175-186.

Valentine, J. R., and K. Heck. 1993. Mussels in seagrass meadows: their influence on macroinvertebrate abundance and secondary production in the Northern Gulf of Mexico. Marine Ecology Progress Series **96**:63-74.

Valiela, I., J. McClelland, J. Hauxwell, P. J. Behr, D. Hersh, and K. Foreman. 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnology and Oceanography **42**:1105-1118.

van de Voorde, T. F. J., W. H. van der Putten, and T. Martijn Bezemer. 2011. Intra- and interspecific plant–soil interactions, soil legacies and priority effects during old-field succession. Journal of Ecology **99**:945-953.

van der Heide, T., L. L. Govers, J. de Fouw, H. Olff, M. van der Geest, M. M. van Katwijk, T. Piersma, J. van de Koppel, B. R. Silliman, A. J. Smolders, and J. A. van Gills. 2012. A three-stage symbiosis forms the foundation of seagrass ecosystems. Science **336**:1432-1434.

van der Heide, T., A. J. P. Smolders, B. G. A. Rijkens, E. H. van Nes, M. M. van Katwijk, and J. G. M. Roelofs. 2008. Toxicity of reduced nitrogen in eelgrass (*Zostera marina*) is highly dependent on shoot density and pH. Oecologia **158**:411-419.

van der Heide, T., E. H. van Nes, G. W. Geerling, A. J. P. Smolders, T. J. Bouma, and M. M. van Katwijk. 2007. Positive feedbacks in seagrass ecosystems: implications for success in conservation and restoration. Ecosystems **10**:1311-1322.

Vernberg, F. J. 1976. Physiological and biochemical adaptations. Pages 333-480 *in* M. Wiley, editor. Estuarine Processes: uses, stresses, and adaptation to the estuary. Academic Press, New York, NY.

Vinther, H. F., J. S. Laursen, and M. Holmer. 2008. Negative effects of blue mussel (*Mytilus edulis*) presence in eelgrass (*Zostera marina*) beds in Flensborg fjord, Denmark. Estuarine, Coastal and Shelf Science **77**:91-103.

Virnstein, R. W., and P. A. Carbonara. 1985. Seasonal abundance and distribution of drift algae and seagrasses in the mid-Indian River Lagoon, Florida. Aquatic Botany **23**:67-82.

Wada, S., M. N. Aoki, Y. Tsuchiya, T. Sato, H. Shinagawa, and T. Hama. 2007. Quantitative and qualitative analyses of dissolved organic matter released from *Ecklonia cava* Kjellman, in Oura Bay, Shimoda, Izu Peninsula, Japan. Journal of Experimental Marine Biology and Ecology **349**:344-358.

Waldbusser, G. G., R. A. Steenson, and M. A. Green. 2011. Oyster shell dissolution rates in estuarine waters: effects of pH and shell legacy. Journal of Shellfish Research **30**:659-669.

Walker, S. E. 1995. Taphonomy of modern and fossil intertidal gastropod associations from Isla Santa Cruz and Isla Santa Fe, Galápagos Islands. Lethaia **28**:371-382.

Wall, C. C., B. J. Peterson, and C. J. Gobler. 2011. The growth of estuarine resources (*Zostera marina*, *Mercenaria mercenaria, Crassostrea virginica*, *Argopecten irradians*, *Cyprinodon variegatus*) in response to nutrient loading and enhanced suspension feeding by adult shellfish. Estuaries and Coasts **34**:1262-1277.

Watson, D. M., and M. Herring. 2012. Mistletoe as a keystone resource: an experimental test. Proceedings of the Royal Society of London B: Biological Sciences **279**:3853-3860.

Waugh, D. A., R. M. Feldmann, R. S. Crawford, S. L. Jakobsen, and K. B. Thomas. 2016. Epibiont preservational and observational bias in fossil marine decapods. Journal of Paleontology **78**:961-972.

Waycott, M., C. M. Duarte, T. J. B. Carruthers, R. J. Orth, W. C. Dennison, S. Olyarnik, A. Calladine, J. W. Fourqurean, K. L. Heck, A. R. Hughes, G. A. Kendrick, W. J. Kenworthy, F. T. Short, S. L. Williams, and R. T. Paine. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proceedings of the National Academy of Sciences of the United States of America **106**:12377-12381.

Wernberg, T., F. Tuya, M. S. Thomsen, and G. Kendrick. 2010. Turban snails as habitat for foliose algae: contrasting geographical patterns in species richness. Marine and Freshwater Research **61**:1237-1242.

Williams, S. L., and M. H. Ruckelshaus. 1993. Effects of nitrogen availability and herbivory on eelgrass (*Zostera marina*) and epiphytes. Ecology **74**:904-918.

Wilson, J. G., and J. W. Fleeger. 2012. Estuarine benthos. Pages 303-325 *in* J. W. Day Jr., B. C. Crump, W. M. Kemp, and A. Yáñez-Arancibia, editors. Estuarine Ecology. John Wiley & Sons, Inc., Hoboken, NJ.

Wilson, K. A., K. W. Able, and K. L. Heck Jr. 1990. Predation rates on juvenile blue crabs in estuarine nursery habitats: evidence for the importance of macroalgae (*Ulva lactuca*). Marine Ecology Progress Series **58**:243-251.

Witman, J. D., and T. H. Suchanek. 1984. Mussels in flow: drag and dislodgement by epizoans. Marine Ecology Progress Series **16**:259-268.

Woods, C. M. C., and D. R. Schiel. 1997. Use of seagrass *Zostera novazelandica* (Setchell, 1933) as habitat and food by the crab *Macrophthalmus hirtipes* (Heller, 1862) (Brachyura: Ocypodidae) on rocky intertidal platforms in southern New Zealand. Journal of Experimental Marine Biology and Ecology **214**:49-65.

Wright, J. T., J. E. Byers, J. L. DeVore, and E. E. Sotka. 2014. Engineering or food? mechanisms of facilitation by a habitat-forming invasive seaweed. Ecology **95**:2699-2706.

Xu, Q., and H. Yang. 2007. Food sources of three bivalves living in two habitats of Jiaozhou Bay (Qingdao, China): indicated by lipid biomarkers and stable isotope analysis. Journal of Shellfish Research **26**:561-567.

Yakovis, E., and A. Artemieva. 2017. Cockles, barnacles and ascidians compose a subtidal facilitation cascade with multiple hierarchical levels of foundation species. Scientific Reports **7**:237.

Zieman, J. C., J. W. Fourqurean, and T. A. Frankovich. 1999. Seagrass die-off in Florida Bay: long-term trends in abundance and growth of turtle grass,*Thalassia testudinum*. Estuaries **22**:460-470.

CHAPTER 2 A GLOBAL REVIEW AND META-ANALYSIS OF EFFECTS OF CO-OCCURRING MACROALGAE, ANGIOSPERMS, AND BIVALVES

Abstract

Globally, freshwater, marine, and estuarine environments share some functionally similar foundation species, such as slow-growing clonal angiosperms, faster growing solitary macroalgae, and shell-forming bivalves. Despite their trait differences these taxa all modify ambient environmental conditions and create habitat, thereby increasing biodiversity. Furthermore, these foundation species often coexist and interact, potentially facilitating or inhibiting each other, and may therefore also have cascading positive or negative impacts on other species. Understanding the magnitude and direction of these interactions is important for restoration and conservation ecologists and scientists. Here I provide a quantitative review and meta-analysis of 96 experiments published in 82 scientific papers that tested two-way interactions between angiosperms (seagrasses and freshwater species), macroalgae, and bivalves. I first identified research gaps and biases, showing that not a single study was reported from South America, and that only three experiments were of longer duration than two years. Furthermore, experiments from freshwater systems were scarce (9%) and few (4%) addressed bivalve-macroalgae interactions. In the meta-analysis I found negative effects of macroalgae, positive effects of bivalves, and no net effect of angiosperms on other foundation species, and that small foundation species (based on maximum size in each organism category) were affected more negatively than larger foundation species. These findings were robust across experimental duration, geographical latitudes, ecosystem types, and experimental conditions, except that the negative effect from macroalgae was more severe in laboratory compared to field experiments. This review and meta-analysis aims to stimulate new research that targets the identified research gaps and provides scientists and managers an overview of the effects of these important aquatic foundation species.

Introduction

Species interactions and foundation species

Communities are dynamic, characterized by complex biotic and abiotic interactions that affect the abundance, growth, survival and reproduction of species. Within communities, organisms can have positive, neutral or negative effects on each other through direct or

indirect pathways. Direct positive effects occur through facilitators, mutualists, habitat-providers, habitat-ameliorators, and stress-reducers (Bertness and Callaway 1994, Bertness and Leonard 1997, Bertness et al. 1999, Stachowicz 2001, Callaway 2002, Tirado and Pugnaire 2005, Altieri et al. 2007, López and Coutinho 2010, Thomsen et al. 2012a, Gribben et al. 2013). Direct negative effects occur through interactions with competitors, herbivores, predators, parasites, and pathogens (Connell 1961, Sih 1985, Price 1986, Mouritsen 2002, Scheibling and Gagnon 2006, Borer et al. 2007).

An organism that creates habitat, mediates interactions, controls populations, and regulates ecosystem dynamics within a community can be considered a foundation species (Dayton 1972, Ellison et al. 2005). These are spatially abundant and provide a buffer to biotic and abiotic stressors in the communities they inhabit (Dayton 1972, Ellison et al. 2005, Angelini et al. 2011, Angelini et al. 2015). For example, trees create structure and alter microclimatic conditions within a forest (Young and Mitchell 1994, Chen and Franklin 1997, Ellison et al. 2005), sea urchins on marine subtidal walls can create biodiversity hotspots within their spines (Altieri and Witman 2014), and on intertidal rocky shores, macroalgae create habitat and buffer wave action (Schiel and Lilley 2007, Schmidt et al. 2011). Multiple foundation species co-occur and interact in ecosystems, creating nested and adjacent assemblages of foundation species (Thomsen et al 2010, Angelini et al 2011), such as trees and epiphytes in forests (Ellwood and Foster 2004, Angelini and Silliman 2014), grasses and *Acacia* trees on African prairies (Riginos et al. 2009), cordgrass and mussels on rocky shores (Altieri et al. 2007), or macroalgae, seagrass, and bivalves in estuaries (Thomsen et al. 2013). However, despite the commonality of co-occurring foundation species, interactions between them have received relatively little research scrutiny (except trophic cascades, e.g., Estes and Palmisano 1974, Carpenter et al. 1985, Ripple and Beschta 2012), and are only recently being systematically researched (e.g., Wahl 2008, Thomsen et al. 2010a, Angelini et al. 2011, Watson and Herring 2012, Thomsen et al. 2013).

Interactions among aquatic angiosperms, macroalgae, and bivalves

Freshwater, marine, and estuarine environments share several types of foundation species, in particular, angiosperms, macroalgae, and bivalves. Aquatic angiosperms (seagrasses and freshwater macrophytes) provide habitat for fish, birds, and other organisms (Orth et al. 1984, Knox 1986), change the water column around them (Fonseca and Cahalan 1992, Sand-Jensen 1998, Engelhardt and Ritchie 2001, Larned 2003, Semesi et al. 2009), stabilize sediments

(Orth 1977, Carr et al. 2010), and are important primary producers, organic carbon producers, and carbon sinks (Duarte and Chiscano 1999, Duarte et al. 2005, Fourqurean et al. 2012). Macroalgae provide similar ecological functions to seagrass, providing food for invertebrates, fish, and marine mammals (Montgomery and Gerking 1980, Dudley et al. 1986, Kumar et al. 2008), creating habitat (Lilley and Schiel 2006, Villegas et al. 2008, Schmidt et al. 2011), acting as nutrient transformers and sinks (Valiela et al. 1997, Fong and Zedler 2000), and facilitating short (Holmquist 1994, Clarkin et al. 2012) and long distance (Ingólfsson 1995, Ólafsson et al. 2001, Nikula et al. 2010) dispersal of other organisms. However, angiosperms and macroalgae differ in key ecological traits. For example, macroalgae have a wide variety of morphologies, require hard substrate to start their benthic life cycle, are typically solitary individuals, and can have high growth rates that under high nutrient levels can result in rapid biomass accumulation, strong shading, and low oxygen levels (Valiela et al. 1997, Raffaelli et al. 1998, Han and Liu 2014, Lyons et al. 2014). Seagrasses are marine angiosperms that often co-occur with macroalgae but differ in morphologies and life histories. They are flat-leaved clonal organisms with lateral vegetative spread (but can also reproduce sexually), and roots and rhizomes that stabilize and accumulate sediments (Walker et al. 2001, Williams and Heck Jr 2001, Orth et al. 2006). Finally, bivalves are benthic foundation species found in streams, rivers, lakes, estuaries, mangroves, salt marshes, and rocky shores. Bivalves occur from the tropics to polar regions and from high elevation lakes to the deepest oceanic trenches. Bivalves provide important linkages between benthic and pelagic systems through their water column filtering and sediment biodeposition (Strayer et al. 1999, Coen et al. 2007). Filter feeding also enhances light penetration and water clarity (Coen et al. 2007, Zu Ermgassen et al. 2013). Finally, bivalves create complex, three-dimensional habitat through their hard calcareous shells (Ricciardi et al. 1997, Gutiérrez et al. 2003, Tolley and Volety 2005, Borthagaray and Carranza 2007), creating ecological legacies long after the organism itself has died (Powell and Davies 1990, Powell et al. 2006, Cuddington 2011).

Angiosperms, macroalgae and bivalves often co-occur in the photic zone in aquatic systems, from tropical to polar regions. However, there is no consensus about how they affect each other, as case studies have demonstrated both positive and negative effects depending on geographic location, invasiveness, season, anthropogenic influence, and other environmental factors (Choat and Schiel 1982, Coma et al. 2000, Broitman et al. 2001, Piola and Johnston 2008, Schiel 2011, Schultz and Dibble 2012, Scherner et al. 2013). In addition, most of the

literature examines one-way interactions (i.e., algal effects on bivalves, see: Irlandi 1997, Ceccherelli and Cinelli 1999, Bologna and Heck 2000, Booth and Heck Jr. 2009); variation in experimental designs, spatio-temporal scales, and taxonomic groupings have made it difficult to identify generalities about these interactions. The lack of an overview on the interactions may imply that it is difficult for ecologists to model and predict how aquatic foundation species affect each other and the ecosystems in which they operate.

Global review and meta-analysis

Systematic reviews and meta-analyses are standardized methods to provide unbiased overviews on research topics, identify research gaps and provide quantitative data about the direction, magnitude and context-dependency of species-interactions. The aim of this chapter is to provide a systematic review and meta-analysis to examine reciprocal effects between aquatic macrophytes, macroalga and bivalves. To do this I searched the peer reviewed literature that, in manipulative experiments, tested effects of these foundation species on each other. Although a few meta-analyses have evaluated effects between aquatic foundation species before, these other studies only tested for unidirectional effects on a subset of interactions, such as seaweed effects on seagrass (Thomsen et al. 2012b), invasive bivalves on their environment (Ward and Ricciardi 2007, Higgins and Zanden 2010), invasive seaweeds on native seaweeds (Thomsen et al. 2009b), or stressors on seagrass (Hughes et al. 2004, McMahon et al. 2013). With this review and meta-analysis, I aim to provide background information and identify research gaps for researchers, conservation managers, restoration engineers, climate scientists, and government bodies to use wherever co-occurring foundation species need to be managed. Specifically, I hypothesized that:

- Angiosperms have positive effects on bivalves because they can reduce water flow (allowing increased juvenile and organic matter settlement) and predation, but negative effects on algae as they compete for space, light and nutrients.
- Macroalgae have negative effects on bivalves and angiosperms because they can shade and smother other benthic species.
- Bivalves have positive effects on angiosperms and macroalgae as they can increase attachment space on shells and nutrients through deposition of faeces and pseudofaeces.

- Small foundation species are affected more strongly than large foundation species because smaller organisms - within a foundation species organism category- have lower resilience to stress and are weaker competitors than larger organisms.
- Latitude, experimental duration, aquatic ecosystem type, and experimental type have, in contrast to the previous listed hypothesis, no consistent modifying effect on the interactions between foundation species (i.e., previous hypotheses are robust to minor variations in spatio-temporal and experimental conditions).

Methods

Data collection

I used Google Scholar and Web of Science online databases to locate published articles that reported 1) a manipulative laboratory or field experiment from an aquatic ecosystem, and 2) effects on an ecological performance response of a focal foundation species, including its abundance (e.g., cover, biomass), size (e.g., length, width), general ecological process (e.g., growth, production, recruitment, survival) and more specific ecological process (e.g., bivalve byssal thread production which is only relevant for bivalves, see Table S1 for details). I examined in detail the first 150 articles (using the unmodified filter "relevance" in both) for each search term or phrase, identified from searches in Google Scholar and Web of Science using the following keywords: 'seagrass*', 'seaweed*', 'bivalve*', 'eelgrass*', 'aquatic', 'macrophyte*', 'experiment', 'SAV', 'vegetation', 'angiosperm*', 'freshwater', '*Dreissena*', 'mussel*', 'clam*', 'macroalga*', '*Mytilus*', '*Ulva*', '*Cladophora*', *'Ruppia*', '*Zostera*' and combinations thereof (such as 'seagrass bivalve experiment'), leading to >20 searches of 150 articles each. Early searches showed that no relevant papers were found after the first 150 papers had been reviewed. I also examined the reference sections of these papers for potentially relevant publications my standardized search may have missed. The literature search took place from November 2016 to April 2017. Titles and abstracts were screened to identify potentially relevant papers. Full manuscripts were then obtained and examined in detail to identify relevant text, tables, and figures for data extraction.

Data extraction and effect size calculation

In total, I examined >1000 unique articles from all combinations of search terms, of which 82 met the two main data criteria. For each of the 82 research papers, I extracted meta-data about

the following moderators: 1) response type (abundance, survival, growth, etc.), 2) interaction type (e.g., macroalgae→bivalve, the order of the reported organisms reflect the independent and dependent variable, respectively), 3) ecosystem (freshwater or marine), 4) experiment type (lab or field experiment), 5) experimental duration (months), 6) latitude of study location, and 7) organismal size. Organismal size was grouped into small, medium and large organisms based of the maximum size reported from online scientific resources (such as AlgaeBase) or published taxonomic guides; Angiosperms: <22, 22-40, ≥41 cm; Macroalgae <15, 15-40, ≥41 cm; Bivalves <8, 9-14, ≥ 15 cm.

I extracted all relevant data, including multiple reported responses within a study and controls. The 'controls' referred to plots with only a single foundation species. For example, if an experiment tested for effects of a seaweed on a seagrass, the control would be the 'seagrass only' plots. All responses were extracted from experiments that reported multiple responses (such as those impacting many individual taxa). For experiments with repeated measures, I extracted all points through time to get a better estimate of the effect size metric when aggregating effects (see next section). For each identified experiment, I extracted mean values, sample sizes (replication levels), and statistical variation (SE, SD, or CI) from the text, tables, and figures using an online data extractor (WebPlotDigitizer, https://automeris.io/WebPlotDigitizer/). Extracted error values were recalculated to standard deviations. I used, like many ecological meta-analyses, Hedges' g (Hedges 1981) as the standardized effect size metric (i.e., Arft et al. 1999, Rustad et al. 2001, Levine et al. 2004, Guy-Haim et al. 2018). Hedges' g is similar to Cohen's *d*, but applies a correction factor to get an unbiased effect size estimator (Borenstein et al. 2011, Del Re 2015). Hedges' g (Hedges 1981) was calculated as:

$$\text{Eq 1. } g = \left(\frac{FS_{independent\ and\ dependent\ present} - FS_{dependent\ only}}{S}\right) \times \left(1 - \frac{3}{4df-1}\right)$$

where *FS* stands for foundation species, *S* is the pooled standard deviation and *df* is the degrees of freedom used to calculate *S*. Analyses were weighted by the sum of the inverse variance in each study and the variance pooled across studies and therefore gave greater weight to those studies with higher replication and lower data dispersion. Negative g-values correspond to negative effects on the dependent foundation species (inverse responses, like mortality, were multiplied by -1, to ensure uniformity with survival, abundance, growth and reproduction) (Borenstein et al. 2011).

Meta-analysis

Dependent effect sizes from each publication were aggregated and averaged using the Borenstein, Hedges, Higgins, and Rothstein (BHHR) procedure to reduce bias (Borenstein et al. 2011), as recommended by Hoyt and Del Re (2018). I used random-effects models with restricted maximum likelihood methods for each analysis (Thompson and Sharp 1999, Hoeksema et al. 2010, Borenstein et al. 2011, Del Re 2015, Guy-Haim et al. 2018) and tested for publication bias with funnel plots using trim-and-fill analysis (Duval and Tweedie 2000) and Egger's regression tests (Egger et al. 1997). Publication bias can occur for many reasons but is particularly problematic as small or non-significant effects are less likely to be published (Rothstein et al. 2006). Publication bias is likely to occur if a funnel plot shows strong asymmetry around the mean effect size and/or if Egger's regression test is significant.

I extracted and calculated 1401 non-independent effect sizes from 96 independent experiments in 82 publications, subsequently aggregated and averaged into 242 independent effect sizes ($g_{individual}$). All performance responses (abundance, size, general process, specific process) were found in the literature for all interacting foundation species (see Table S1). I interpreted the magnitude of the effect sizes to be 'small' ($g \approx 0.2$, effect not visible to the naked eye), 'medium' ($g \approx 0.5$, effect visible to naked eye) or 'large' ($g \approx 0.8$) as recommended by Cohen (1988). If effect size 95% confidence intervals did not overlap with zero or each other, effects were considered statistically significant.

Analyses were done using R Statistical Software (version 3.4.2), with the packages 'MAd' and 'metafor', as detailed in Del Re (2015). Funnel plots and bias analyses, as well as tables of models, fits, and heterogeneity can be found for all moderator variables in the Supplementary material.

Results

Global review

The 82 studies were carried out in 20 countries (Figure 2.1), dominated by studies from the Northern Hemisphere (73), with most studies taking place in the United States (39) and Europe (28). The temperate and subtropical climate zones were overrepresented (50 and 31 studies respectively), whereas polar and tropical zones were represented by one study each (Fig. 2.2A). There were 96 directional interactions in the 82 studies: 28

macroalgae→angiosperm, 9 angiosperm→macroalgae, 18 macroalgae→bivalve, 4 bivalve→macroalgae, 24 angiosperm→bivalve, and 13 bivalve→angiosperm (Fig. 2.2B, the arrow indicates the direction of the interaction). Freshwater experiments were scarce compared to marine studies (9 vs. 87, Fig. 2.2B). Publications about experimental manipulations between macroalgae, angiosperms, or bivalves were commonly studied in the early 1990s, and follow a bimodal distribution, with a peak in publications in the early 2000s and again in the early 2010s (Fig. 2.2C). The experimental durations ranged from 2.42 hours to 4.2 years (0.003 to 50 months) with a median experimental duration of 2.25 months (Figure 2.2D).

Meta-analysis

Foundation species interactions

Angiosperms had a small negative effect on macroalgae (g = -0.183 ± 0.492 95% CI, reported as Hedge's g ± 95% CI hereafter) and a medium positive effect on bivalves (g = 0.462 ± 0.558) but none were significantly different from zero (p = 0.466, p = 0.105 respectively, Figure 2.3A). By contrast, macroalgae had significant negative effects on both angiosperms (g = -1.127 ± 0.285, p < 0.001) and bivalves (g = -0.471 ± 0.289, p = 0.001, Figure 2.3A). Finally, bivalves had positive effect on both macroalgae (g = 0.092 ± 0.366, p = 0.486) and angiosperms (g = 0.524 ± 0.429, p = 0.017) but only the latter was significantly different from zero.

Size of dependent foundation species

Small foundation species were negatively affected by angiosperms (g = -0.009 ± 0.809, p = 0.982), macroalgae (g = -1.444 ± 0.511, p < 0.001), and bivalves (g = -0.501 ± 0.311, p = 0.002, Figure 2.3B) although effects of angiosperms were not significantly different from zero. By comparison, effects on medium and large foundation species were less negatively affected by angiosperms (medium, g = 0.264 ± 0.435, p = 0.236, large, g = 1.105 ± 3.516, p = 0.538), macroalgae (medium, g = -0.761 ± 0.447, p = 0.001, large, g = -0.680 ± 0.212, p<0.001), or bivalves (medium, g = 0.484 ± 0.604, p = 0.117, large g = 0.525 ± 0.455, p = 0.024, Figure 2.3B). More specifically, small foundation species were significantly more negatively affected than large foundation species for both macroalgae and bivalves (i.e., the confidence limits did not overlap each other).

Experiment type and ecosystem

Effects of angiosperms were small and positive for both field (g = 0.247 ± 0.466, p = 0.300) and lab experiments (g = 0.269 ± 0.268, p = 0.049, Figure 2.3C) in both marine (g = 0.290 ± 0.466, p = 0.223) and freshwater (g = 0.144 ± 0.395, p = 0.598, Figure 2.3D) systems. There were no differences between the two effect sizes for experimental type or ecosystem (Figure 2.3C, D). Macroalgae had negative effects on other foundation species in both field (g=-0.541 ± 0.212, p < 0.001, Figure 2.3C) and laboratory (g = -1.597 ± 0.430, p < 0.001) experiments, and in both freshwater (g = -1.016 ± 1.172, p = 0.089) and marine (g = -0.893 ± 0.215, p < 0.0041, Figure 2.3D) systems. However, effect sizes were shown to be different from each other between lab and field (Figure 2.3C), but not ecosystem (Figure 2.3D). Bivalves had strong, significant, positive effects in laboratory experiments (g = 1.044 ± 0.906, p = 0.024) and field experiments (g = 0.314 ± 0.372, p = 0.098), and there was no significant difference between the two types (Figure 2.3C). Finally, effects from bivalves were small and positive but not significant in freshwater systems (g = 0.227 ± 1.142, p = 0.696) and medium and positive and significant in marine systems (0.476 ± 0.374, p = 0.011), and again there was no significant difference in effect size between the two ecosystems.

Latitude and experimental duration

Geographic latitude or experimental duration did not modify effect sizes (Hedges g = -0.578 + 0.005 × Latitude, p = 0.517, Figure 2.4A; Hedges g = -0.346 + -0.005 × Experimental duration, p = 0.702, Figure 2.4B). The few effect sizes that were reported near the equator or the poles focused on effects from angiosperms or bivalves, respectively. Furthermore, only a few effect sizes were from experiments exceeding 1.5 years, except for two experiments with angiosperms and six experiments with bivalves (Figure 2.4B).

Discussion

Global review

This review of interactions between aquatic angiosperms, macroalgae, and bivalves provides the first quantitative overview of how these foundation species affect each other and highlight key research gaps. First, I found, like many other reviews (Figure 1, Figure 2A, Platnick 1991, Wilson et al. 2007, Pyšek et al. 2008, Martin et al. 2012, Trimble and van Aarde 2012,

Thomsen et al. 2014, Mundim and Bruna 2016) a latitudinal/geographic bias because most experiments were conducted in temperate and subtropical climate zones. This bias partly arises because more research institutions, universities, funding options and researchers occur in economically richer mid-latitudinal countries (Pyšek et al. 2008, Martin et al. 2012) partly because these regions are often logistically less complicated to work in (Wilson et al. 2007, Pyšek et al. 2008, Martin et al. 2012), or different foundation species not covered in this review (such as corals and macroalgae) are more the focus of the regions not found in this review. However, angiosperms, bivalves, and macroalgae are common and coexist in both tropical and cold waters (Pielou 1977, Orth et al. 2006, Gosling 2008, Hurd et al. 2014) and more experiments should be done in these regions to provide a more general ecological understanding of these interactions and help prioritize conservation and restoration projects (Martin et al. 2012).

Many more experiments were done in marine compared to freshwater systems (75 vs 8, Figure 2.2B). All three types of foundation species are common in freshwater systems (Graf and Cummings 2007, Karatayev et al. 2007, Chambers et al. 2008, Bellinger and Sigee 2015), highlighting an important research gap. Under-representation of freshwater experiments may be a long-standing problem; in a review of trophic field experiments there was a "total lack of manipulations of herbivores...and non-arthropod invertebrates in freshwater" (Sih 1985) and other studies have found freshwater experiments to be under-represented compared to marine and terrestrial experiments (i.e., Connell 1983, Schoener 1983, Gurevitch et al. 1992, Thompson et al. 2013). Freshwater systems are vulnerable to anthropogenic stressors, such as climate change (IPCC 2007, Woodward et al. 2010, Markovic et al. 2017) and it is therefore important to understand how these systems will change in the future. Without baseline experimentation to document interactions among angiosperms, macroalgae, and bivalves in the current climate, ecologists will not be able to identify how these interactions and communities may be altered in the near future.

Long term experiments were also scarce as ca. 80% were of less than 6 months and only 13% ran for a year or longer (Figure 2.2D). However, many ecologists argue that much longer experiments are needed to incorporate natural weather phenomena, climate variability, and natural organismal cycles (Tilman 1989, Jackson and Füreder 2006), although the timeframe should be adjusted to study organisms (e.g., less time is needed to experimentally document impacts on plankton than trees (Strayer et al. 1986, Tilman 1989)). Having long-term experimental data will aid in identifying true species-interaction effects from background

environmental noise (see Tilman 1989, Magnuson 1990 for reviews), of particular relevance for long lived bivalves and clonal seagrass. However, long-term experiments are typically limited by short-term funding cycles, and are more likely to be affected by demonic intrusions and natural or anthropogenic disturbances (Hurlbert 1984, Turner et al. 2003, Ilg et al. 2008, Birkhead 2014).

Meta-analysis

Effects from angiosperms

Marine angiosperms such as seagrass are important foundation species for shallow water systems and provide essential ecosystem services including habitat formation, carbon sinks, nursery habitat, and high productivity (Orth et al. 2006). Similarly, freshwater angiosperms are important in streams and lakes, where they can fix nitrogen (Bristow 1974), facilitate fish and zooplankton (Blindow et al. 2014), increase water quality (Dennison et al. 1993), and create habitat (Dibble et al. 2006). However, freshwater angiosperms can also bloom and become nuisance organisms smothering certain species and negatively affect local economies (Caraco et al. 2006, Chambers et al. 2008).

As hypothesized, I found a small, negative, but non-significant, effect of angiosperms on macroalgae (Figure 2.3A). Negative effects may arise due to competition for space, light, or nutrients (Kiirikki 1996, Ceccherelli and Cinelli 1999, Ceccherelli et al. 2000, Davis and Fourqurean 2001, Taplin et al. 2005). The lack of significance could be caused by large data variability (indicating that in some cases facilitation may cancel inhibition), and/or relatively low replication levels. Importantly, these effects were based only on marine systems. Angiosperms, such as *Elodea, Ruppia, and Vallisneria* spp., and macroalgae like *Mougeotia, Cladophora, and Chara* spp., commonly coexist in freshwater habitats (Shili et al. 2002, Schutten et al. 2005, Lürling et al. 2006), suggesting that these interactions should be studied experimentally. By contrast, I found a positive, albeit not significant, effect of angiosperms on bivalves (the relatively large 95% confidence limits overlapped slightly with zero, see Figure 2.3A). This positive effect may occur where angiosperms provide substrate for settling bivalve recruits, reduce predation, and increase deposition of sediments and organic matter (Irlandi et al. 1995, Irlandi 1996, Irlandi 1997, Peterson and Heck Jr 2001b, Fritz et al. 2004). Again, freshwater systems were under-represented (Figure 2.2B), which is problematic because freshwater bivalves often coexist with angiosperms (Aldridge 2000, Bringolf et al. 2007, Archambault et al. 2015).

There was a tendency for effects of angiosperms to be more negative with decreasing size of the impacted foundation species (but note that the large 95% confidence limits associated with impacts on large foundation species implied that this tendency was not significant, see Figure 2.3B). Size-dependent effects could occur due to size-refugia of organisms. For example, Peterson (1982) found that disturbances and diseases more negatively affected small than large clams like *Chione cancellata* and *Mercenaria mercenaria*, although predators here targeted larger clams. In freshwater systems, the presence of angiosperms decreased predation of *Dreissena polymorpha* from crayfish, but in this experiment small mussels were eaten more than larger individuals (MacIsaac 1994). Finally, I found that neither ecosystem nor experimental type affected effect sizes, that is, effects were very similar between field, lab, marine and freshwater systems (Figure 2.3C, D). This suggests that the few laboratory experiments that have manipulated angiosperms (e.g., Carpenter 1996, Calisi and Bentley 2009) have mimicked natural scenarios well.

Effects from macroalgae

Macroalgae in marine and freshwater systems facilitate other species by reducing environmental stress and predation and providing attachment space for epibiota and food for grazers (Power 1990, Sogard and Able 1991, Vázquez et al. 1998, Bertness et al. 1999, Schmidt et al. 2011, Dijkstra et al. 2012, Thomsen et al. 2012a). However, macroalgae can also comprise 'nuisance' algal blooms which may cause ecological and economical damage. During a bloom, dense algal mats decrease light and nutrients in the water column (Raffaelli et al. 1998, McGlathery 2001, Lyons et al. 2014) and can lead to anoxic conditions when the mat decomposes (Valiela et al. 1997, Raffaelli et al. 1998, Han and Liu 2014) with negative impacts on the underlying benthic communities. More specifically, I found, as hypothesized, that macroalgae had negative effect on angiosperms (Figure 2.3A), as also shown (with a smaller data-set) in Thomsen et al. (2012b). Although this interaction was well-studied (Figure 2.2B) freshwater systems were again under-represented, with only 7 effects reported from a single study (Ozimek et al. 1991). The strong negative effect reported was particularly evident in the many experiments on bloom-forming *Ulva* species (e.g., Everett 1994, Brun et al. 2003b, Marsden and Maclaren 2010). As algal blooms are likely to become more prevalent (Heisler et al. 2008, Hallegraeff 2010, Harley et al. 2012), seagrass declines (Orth et al. 2006) are likely to continue or even accelerate, and highlight the importance of

quantifying these interactions experimentally, particularly in under-represented freshwater systems and at low and high latitudes.

Macroalgae also had, as hypothesized, negative effects on bivalves, albeit significantly less severe compared to the impacts on angiosperms (Figure 2.3C). Again, during nuisance blooms, macroalgae can physically smother filter- or deposit-feeding bivalves and cause anoxia that stress bivalves physiologically (Thiel et al. 1998, Marsden and Bressington 2009, Marsden and Maclaren 2010). In addition, macroalgae can attach to and grow on bivalve shells, which may stress bivalves physiologically (e.g., by reducing filtering capacities) but also increases drag and thereby the risk of dislodgement due to hydrodynamic forces (O'Connor et al. 2006, Ansell et al. 2009, Box et al. 2009). Again, freshwater studies were under-represented, with only a single experimental effect size (Folino-Rorem et al. 2006, Figure 2.3B).

It was also found, as hypothesized, that macroalgae affected small foundation species more negatively (Norkko et al. 2000, Folino-Rorem et al. 2006, Holmer et al. 2011) than large foundation species (Thiel et al. 1998, Eklöf et al. 2006, Hessing-Lewis et al. 2011, Figure 2.3B), as previously reported for effects on seagrass (Thomsen et al. 2012b). The reason for the more negative effects on small organisms could be due to physical whiplash or scouring effects of macroalgae. For example, intertidal seaweed canopies of *Ascophyllum nodosum* can scour small barnacle recruits and juveniles from adjoining areas (Leonard 1999, Jenkins and Hawkins 2003). Other factors, such as nuisance algae blooms (as described above) that can lead to issues such as reduced light/food availability (Raffaelli et al. 1998, Lamote and Dunton 2006, Holmer et al. 2011), or increased drag on organisms that seaweed epiphytizes (Witman and Suchanek 1984, Wahl 1997) also likely negatively affect small organisms more than large organisms.

Finally, I found that these negative effects from macroalgae were, as hypothesized, similar between freshwater and marine systems (Ozimek et al. 1991, Cummins et al. 2004). However, effects were more negative in the laboratory (Brun et al. 2003b, Holmer et al. 2011) than in the field (Maciá 2000, Marsden and Maclaren 2010, Figure 2.3C, D), so the hypothesis was rejected. The much stronger negative effect from the lab experiments may arise because of strict conditions applied, which may not always mimic natural conditions. For example, Ozimek et al. (1991) used naturally occurring biomasses of both macroalgae and angiosperms in their experiment, but the microcosms could not simulate natural lake

conditions, such as wave action, which plays a large part (e.g., reduces stress of angiosperms) in the natural interactions of those two foundation species. Other laboratory experiments also likely have this issue, so caution must be used by extrapolating highly controlled experimental conditions to more variable field conditions.

Effects from bivalves

Bivalves are important to benthic communities because they can link benthic and pelagic processes, filter and clarify the water column, fertilize the benthos, and provide complex three-dimensional habitat (MacIsaac 1996, Strayer et al. 1999, Norkko et al. 2001, Newell 2004, Norkko et al. 2006). There was, as hypothesized, strong positive effects on angiosperms and little effect on macroalgae (this latter effect size had low sample size and therefore low test-power, Figure 2.3A). Bivalve-angiosperm interactions can therefore be mutualistic, as angiosperms also had positive effects on bivalves (Peterson and Heck Jr 2001b, van der Heide et al. 2012, de Fouw et al. 2016, Sanmartí et al. 2018). Positive effects from bivalves on angiosperms may arise from fertilization by pseudofaeces (Reusch and Williams 1998, Peterson and Heck Jr 1999, 2001b, a, Wall et al. 2008, Booth and Heck Jr. 2009), reduction in sulphides (Reynolds et al. 2007, van der Heide et al. 2012), reducing wave impacts and erosion (Smith et al. 2009), and by clarifying the water column allowing more light to penetrate (Strayer et al. 1999, Newell 2004, Newell and Koch 2004, Grabowski and Peterson 2007).

The non-significant effect on macroalgae was based on only 10 effect sizes extracted from just 4 publications (Kotta et al. 2009, Ward and Ricciardi 2010, Thomsen et al. 2013, Thiet et al. 2014, Figure 2.2B). Given that bivalves and macroalgae co-occur across latitudes, ecosystems and biogeographical regions (Pielou 1977, Gosling 2008, Hurd et al. 2014), clearly more studies should experimentally document impacts of bivalves on macroalgae. This is particularly important because bivalves (such as endangered Unionid mussels and the invasive zebra mussel *Dreissena*) and algae (*Cladophora, Ulva, Caulerpa*) are important ecosystem transformers and shapers (Strayer et al. 1999, Rai et al. 2000, Newell 2004, Limburg et al. 2010). In addition, bivalves also facilitate macroalgae by creating a hard substrate on which macroalgae live on (Thomsen et al. 2010a, Banach-Esteve et al. 2015, Thomsen et al. 2016).

Interestingly, although bivalves generally had positive effects on angiosperms and macroalgae, bivalves nevertheless had a significant negative effect on small foundation

species, although this effect came from 3 effect sizes from 1 publication (Booth and Heck Jr. 2009, Figure 2.3B). In this experiment, high densities of the oyster *Crassostrea virginica* (150 m^{-2}) in a *Halodule wrightii* bed significantly reduced seagrass growth, biomass, and shoot density, likely due to sediment and sulphide build-up (from faeces and pseudofaeces) within the oyster beds, suffocating the seagrass underneath and in close proximity (Booth and Heck Jr. 2009).

Finally, the hypothesis that ecosystem and experiment type would not moderate effect sizes was supported, as effect sizes were similar (overlapping confidence limits) between field (Peterson and Heck Jr 2001a, Carroll et al. 2008) and lab experiments (Wall et al. 2008, van der Heide et al. 2012) in both marine (Reusch et al. 1994, Thomsen et al. 2013) and freshwater systems (Posey et al. 1993, He et al. 2014, Figure 2.3C, D). However, it is again important to note that freshwater experiments were highly under-represented and given the importance of freshwater bivalves as indicator species of environmental quality and pollution (Burns and Smith 1981, Elder and Collins 1991, Carroll et al. 2009) and that they are under increasing anthropogenic stress, more experiments need to be conducted in these systems. Freshwater bivalves are also highly diverse, common, and in the case of Unionids, threatened globally (Graf and Cummings 2007), yet there is little experimental research on their interactions with macroalgae and angiosperms (but see Posey et al. 1993, Kaenel et al. 1998, Fritz et al. 2004, He et al. 2014), and many experiments focusing on one species, the invasive zebra mussel *Dreissena polymorpha* (MacIsaac 1994, Folino-Rorem et al. 2006, Ward and Ricciardi 2010).

Geographic latitude and experiment length

As hypothesized, geographic latitude and experimental duration did not modify effect sizes, highlighting that the effect of one foundation species on another are relatively consistent in space and time. However, and as discussed earlier, few experiments were done at tropical and polar latitudes, revealing research bias towards the middle latitudes (Figure 2.4A). Other ecological meta-analyses have found similar effect sizes across latitudes, such as invertebrate abundance and richness from foundation species (Thomsen et al. 2018b), treeline advancement of forests (Harsch et al. 2009), and soil respiration (Rustad et al. 2001). It is likely these analyses had similar latitudinal bias, perhaps contributing to the lack of significance. Similarly, there were very few long term experiments skewing the regression against experimental duration towards short-term experiments (Figure 2.4B). Meta-analyses

and reviews have long emphasized the need for more long-term experiment datasets (see Global Review section above) to provide more realistic effects. For example, Gurevitch et al. (1992) suggest that the high variation in short experimental length effect sizes could be because a higher diversity of organisms are studied for shorter lengths of time, which will naturally yield more variation; and I did find this result in the experimental length analysis (Figure 2.4B).

Conclusions

I reviewed 82 peer-reviewed publications that in manipulative field or laboratory experiments reported effects of one aquatic foundation species on another. Analyses of these studies revealed important research gaps, in particular, that more experiments should be conducted in non-temperate climates, in freshwater systems, and examine effects of bivalves on macroalgae. My meta-analysis of 242 independent effect sizes documented that, averaged across studies, aquatic angiosperms did not affect macroalgae or bivalves, macroalgae had negative effects on both angiosperms and bivalves, and bivalves had positive effects on angiosperms but no effects on macroalgae. Furthermore, small foundation species were generally more negatively affected than large foundation species. I hope this review and meta-analysis will stimulate new research to fill the outlined research gaps and provide scientists and ecosystem managers with an overview of the literature of these important organisms.

Figures

Figure 0.1 Location of experiments published in 82 scientific papers reporting reciprocal impacts of angiosperms, macroalgae, or bivalves on each other, and therefore included in this review and meta-analysis.

Figure 0.2 Number of peer-reviewed publications used in this review and meta-analysis classified by (A) climate zones (polar ≥66°, temperate = 65-36°, subtropical = 35-23°, tropical = 22-0°), (B) marine and freshwater systems for different types of interactions (the first organism is the independent and the second is the dependent; Alg = macroalgae, Ang = angiosperms, Biv = bivalves), (C) year of publication and (D) experimental duration.

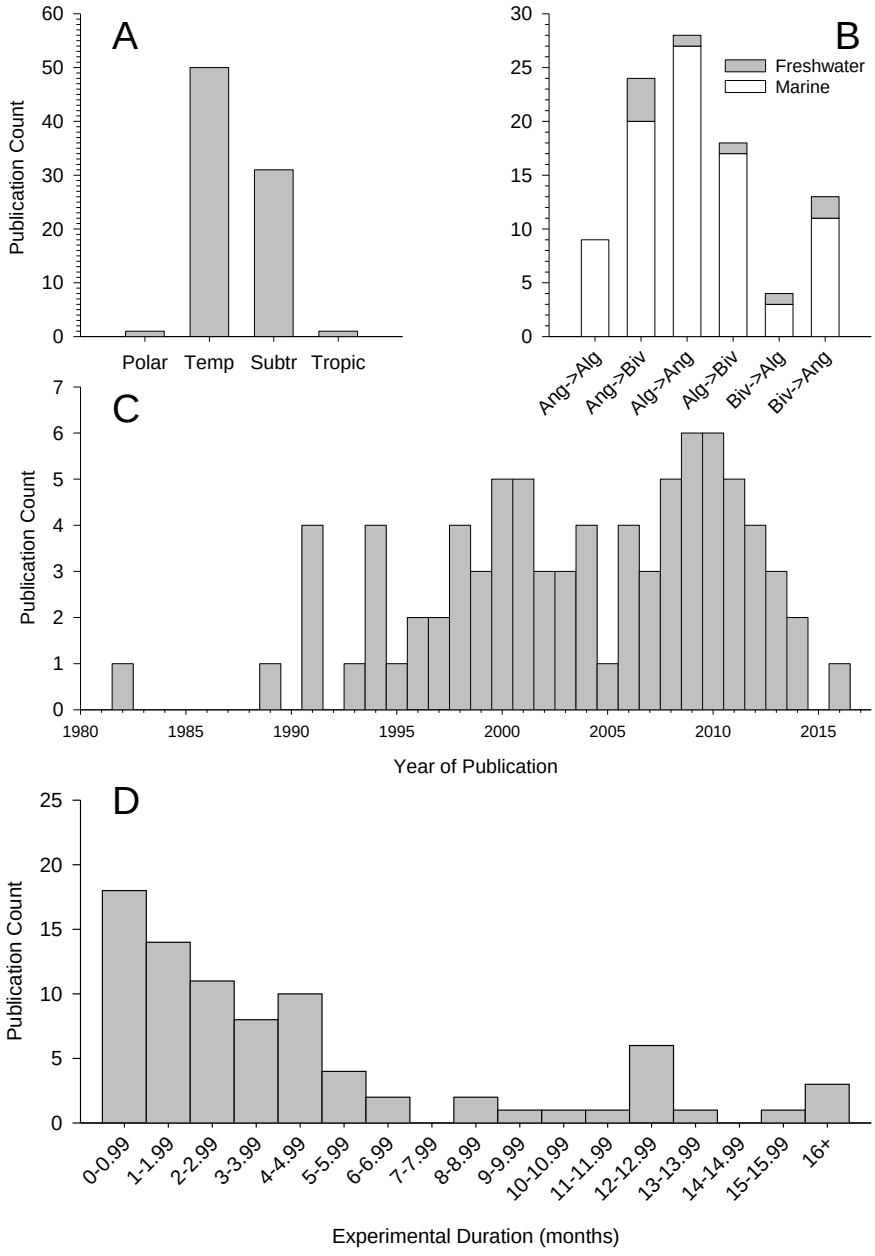


Figure 0.3 Meta-analysis. Hedge's *g* effect sizes ± 95% CI quantifying impacts of angiosperms (Ang), macroalgae (Alg), and bivalves (Biv) (A) on other aquatic foundation species, (B) on small (Sm), medium (Med) and large (Lg) foundation species, (C) in field or laboratory (Lab) experiments and (D) in marine (Mar) or freshwater (FW) systems. Negative values are considered antagonistic interactions, while positive effects are facilitative. The numbers of independent effect sizes used to calculate average effect sizes and confidence intervals are shown in parentheses.

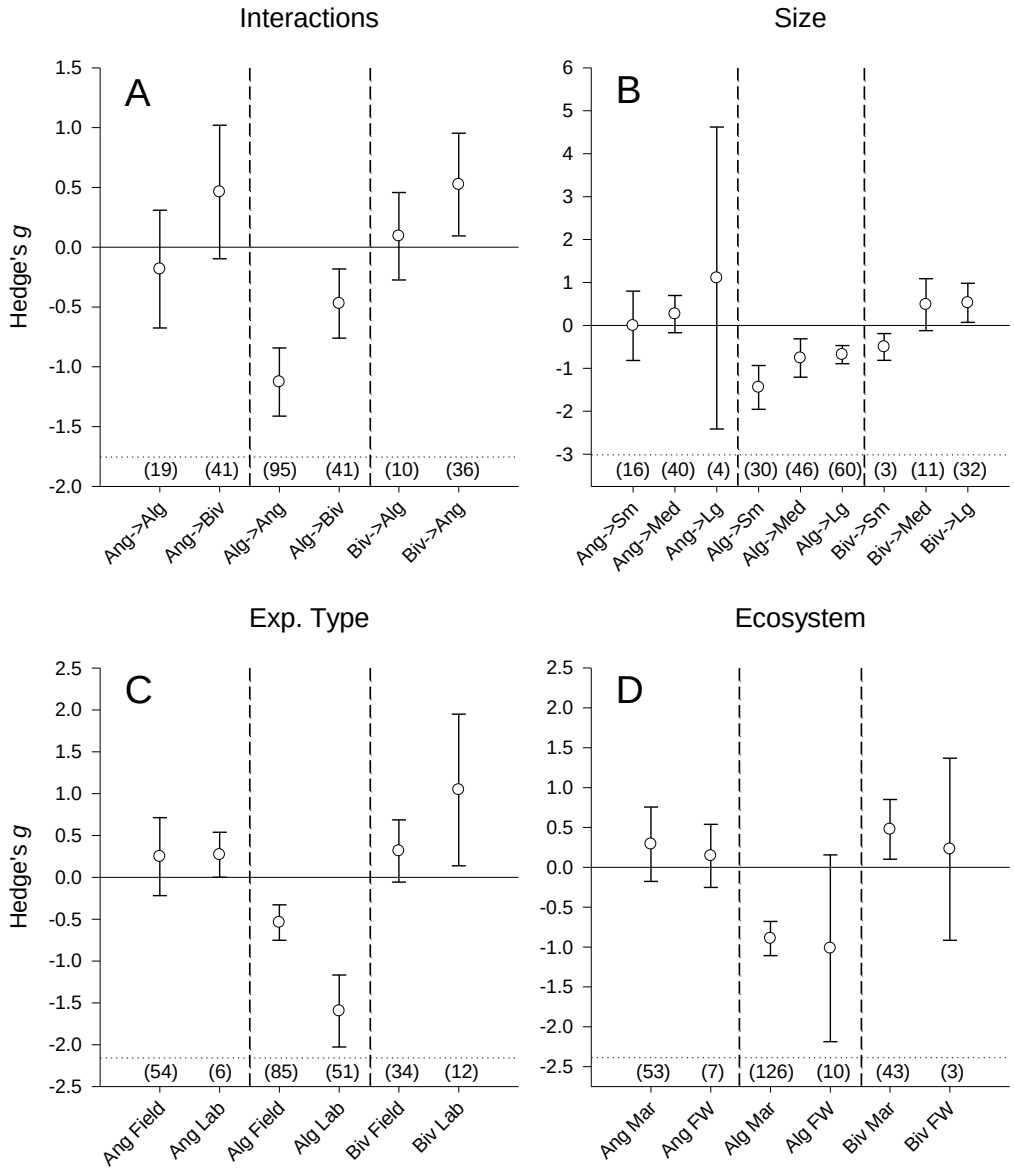
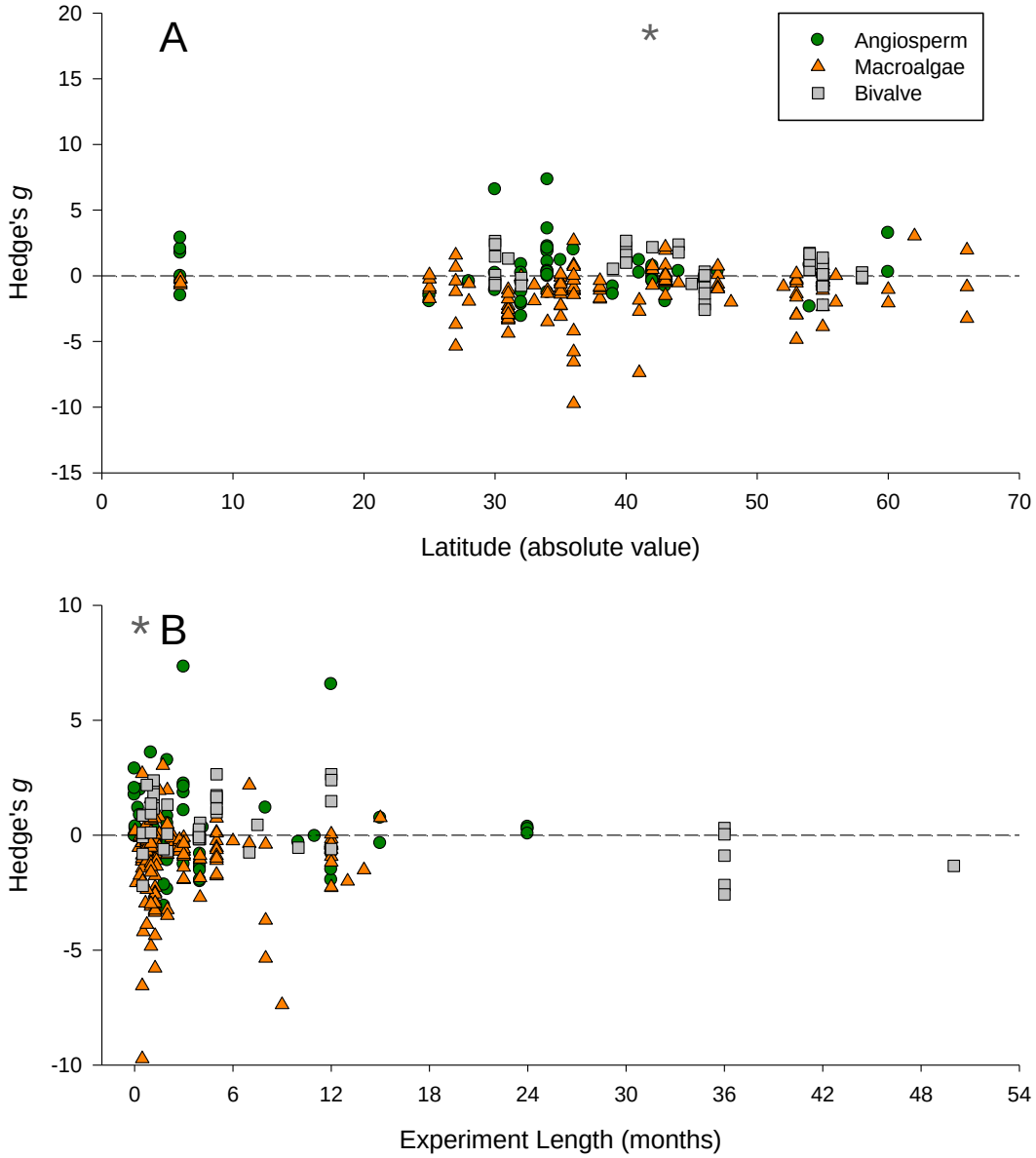


Figure 0.4 Meta-analysis. Hedge's *g* effect sizes quantifying impacts of angiosperms, macroalgae, and bivalves moderated by (A) geographic latitude (absolute value, $g = 0.578 + 0.005 \times \text{Latitude}$, p = 0.517, * = 42, 39.21 outlier) and (B) experimental duration ($g = -0.346 - 0.005 \times \text{Exp. Length}$, p = 0.702, * = 0.75, 39.21 outlier).



References

Aldridge, D. C. 2000. The impacts of dredging and weed cutting on a population of freshwater mussels (Bivalvia: Unionidae). Biological Conservation **95**:247-257.

Altieri, A. H., B. R. Silliman, and M. D. Bertness. 2007. Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. The American Naturalist **169**:195-206.

Altieri, A. H., and J. D. Witman. 2014. Modular mobile foundation species as reservoirs of biodiversity. Ecosphere **5**:1-11.

Angelini, C., A. H. Altieri, B. R. Silliman, and M. D. Bertness. 2011. Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. BioScience **61**:782-789.

Angelini, C., and B. R. Silliman. 2014. Secondary foundation species as drivers of trophic and functional diversity: evidence from a tree–epiphyte system. Ecology **95**:185-196.

Angelini, C., T. van der Heide, J. N. Griffin, J. P. Morton, M. Derksen-Hooijberg, L. P. Lamers, A. J. Smolders, and B. R. Silliman. 2015. Foundation species' overlap enhances biodiversity and multifunctionality from the patch to landscape scale in southeastern United States salt marshes. Proceedings of the Royal Society B **282**:20150421.

Ansell, A. D., L. Robb, and H. T. Powell. 2009. Algal-induced dislodgement as a cause of bivalve mortality on some Scottish beaches. Journal of the Marine Biological Association of the United Kingdom **68**:219-233.

Archambault, J. M., C. M. Bergeron, W. G. Cope, R. J. Richardson, M. A. Heilman, J. E. Corey, M. D. Netherland, and R. J. Heise. 2015. Sensitivity of freshwater molluscs to hydrilla-targeting herbicides: providing context for invasive aquatic weed control in diverse ecosystems. Journal of Freshwater Ecology **30**:335-348.

Arft, A. M., M. D. Walker, J. Gurevitch, J. M. Alatalo, M. S. Bret-Harte, M. Dale, M. Diemer, F. Gugerli, G. H. R. Henry, M. H. Jones, R. D. Hollister, I. S. Jonsdottir, K. Laine, E. Levesque, G. M. Marion, U. Molau, P. Molgaard, U. Nordenhall, V. Raszhivin, C. H. Robinson, G. Starr, A. Stenstrom, M. Stenstrom, O. Totland, P. L. Turner, L. J. Walker, P. J. Webber, J. M. Welker, and P. A. Wookey. 1999. Responses of Tundra Plants to Experimental Warming: Meta-analysis of the international tundra experiment. Ecological Monographs **69**:491-511.

Banach-Esteve, G., M. V. Luis, and S. Deudero. 2015. Temporal trends in sessile epibionts of the endemic bivalve *Pinna nobilis*: variability in *Lophocladia lallemandii* colonization. Thalassas **31**:19-29.

Bellinger, E. G., and D. C. Sigee. 2015. Freshwater algae: identification and use as bioindicators. John Wiley & Sons.

Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. Trends in Ecology & Evolution **9**:191-193.

Bertness, M. D., and G. H. Leonard. 1997. The role of positive interactions in communities: lessons from intertidal habitats. Ecology **78**:1976-1989.

Bertness, M. D., G. H. Leonard, J. M. Levine, P. R. Schmidt, and A. O. Ingraham. 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. Ecology **80**:2711-2726.

Birkhead, T. 2014. Stormy outlook for long-term ecology studies. Nature **514**:405.

Blindow, I., A. Hargeby, and S. Hilt. 2014. Facilitation of clear-water conditions in shallow lakes by macrophytes: differences between charophyte and angiosperm dominance. Hydrobiologia **737**:99-110.

Bologna, P. A., and K. L. Heck. 2000. Impacts of seagrass habitat architecture on bivalve settlement. Estuaries **23**:449-457.

Booth, D. M., and K. L. Heck Jr. 2009. Effects of the American oyster *Crassostrea virginica* on growth rates of the seagrass *Halodule wrightii*. Marine Ecology Progress Series **389**:117-126.

Borenstein, M., L. V. Hedges, J. P. Higgins, and H. R. Rothstein. 2011. Introduction to meta-analysis. John Wiley & Sons, Hoboken, NJ.

Borer, E. T., P. R. Hosseini, E. W. Seabloom, and A. P. Dobson. 2007. Pathogen-induced reversal of native dominance in a grassland community. Proceedings of the National Academy of Sciences **104**:5473-5478.

Borthagaray, A. I., and A. Carranza. 2007. Mussels as ecosystem engineers: their contribution to species richness in a rocky littoral community. Acta Oecologica **31**:243-250.

Box, A., A. Sureda, and S. Deudero. 2009. Antioxidant response of the bivalve *Pinna nobilis* colonised by invasive red macroalgae *Lophocladia lallemandii*. Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology **149**:456-460.

Bringolf, R. B., W. G. Cope, C. B. Eads, P. R. Lazaro, M. C. Barnhart, and D. Shea. 2007. Acute and chronic toxicity of technical-grade pesticides to glochidia and juveniles of freshwater mussels (Unionidae). Environmental Toxicology and Chemistry **26**:2086-2093.

Bristow, J. M. 1974. Nitrogen fixation in the rhizosphere of freshwater angiosperms. Canadian Journal of Botany **52**:217-221.

Broitman, B. R., S. A. Navarrete, F. Smith, and S. D. Gaines. 2001. Geographic variation of southeastern Pacific intertidal communities. Marine Ecology Progress Series **224**:21-34.

Brun, F. G., J. J. Vergara, G. Navarro, I. Hernández, and J. L. Pérez-Lloréns. 2003. Effect of shading by *Ulva rigida* canopies on growth and carbon balance of the seagrass *Zostera noltii*. Marine Ecology Progress Series **265**:85-96.

Burns, K. A., and J. L. Smith. 1981. Biological monitoring of ambient water quality: the case for using bivalves as sentinel organisms for monitoring petroleum pollution in coastal waters. Estuarine, Coastal and Shelf Science **13**:433-443.

Calisi, R. M., and G. E. Bentley. 2009. Lab and field experiments: Are they the same animal? Hormones and Behavior **56**:1-10.

Callaway, R. M. 2002. Positive interactions among alpine plants increase with stress. Nature (London) **417**:844-848.

Caraco, N., J. Cole, S. Findlay, and C. Wigand. 2006. Vascular plants as engineers of oxygen in aquatic systems. BioScience **56**:219-225.

Carpenter, S. R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology **77**:677-680.

Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience **35**:634-639.

Carr, J., P. D'Odorico, K. McGlathery, and P. Wiberg. 2010. Stability and bistability of seagrass ecosystems in shallow coastal lagoons: Role of feedbacks with sediment resuspension and light attenuation. Journal of Geophysical Research: Biogeosciences **115**:1-14.

Carroll, J., C. J. Gobler, and B. J. Peterson. 2008. Resource-restricted growth of eelgrass in New York estuaries: light limitation, and alleviation of nutrient stress by hard clams. Marine Ecology Progress Series **369**:51-62.

Carroll, M. L., B. J. Johnson, G. A. Henkes, K. W. McMahon, A. Voronkov, W. G. Ambrose, and S. G. Denisenko. 2009. Bivalves as indicators of environmental variation and potential anthropogenic impacts in the southern Barents Sea. Marine Pollution Bulletin **59**:193-206.

Ceccherelli, G., and F. Cinelli. 1999. Effects of *Posidonia oceanica* canopy on *Caulerpa taxifolia* size in a north-western Mediterranean bay. Journal of Experimental Marine Biology and Ecology **240**:19-36.

Ceccherelli, G., L. Piazzi, and F. Cinelli. 2000. Response of the non-indigenous *Caulerpa racemosa* (Forsskål) J. Agardh to the native seagrass *Posidonia oceanica* (L.) Delile: effect of density of shoots and orientation of edges of meadows. Journal of Experimental Marine Biology and Ecology **243**:227-240.

Chambers, P. A., P. Lacoul, K. J. Murphy, and S. M. Thomaz. 2008. Global diversity of aquatic macrophytes in freshwater. Hydrobiologia **595**:9-26.

Chen, J., and J. F. Franklin. 1997. Growing-season microclimate variability within an old-growth Douglas-fir forest. Climate Research **8**:21-34.

Choat, J. H., and D. R. Schiel. 1982. Patterns of distribution and abundance of large brown algae and invertebrate herbivores in subtidal regions of northern New Zealand. Journal of Experimental Marine Biology and Ecology **60**:129-162.

Clarkin, E., C. A. Maggs, G. Arnott, S. Briggs, and J. D. R. Houghton. 2012. The colonization of macroalgal rafts by the genus *Idotea* (sub-phylum Crustacea; order Isopoda): an active or passive process? Journal of the Marine Biological Association of the United Kingdom **92**:1273-1282.

Coen, L. D., R. D. Brumbaugh, D. Bushek, R. Grizzle, M. W. Luckenbach, M. H. Posey, S. P. Powers, and S. Tolley. 2007. Ecosystem services related to oyster restoration. Marine Ecology Progress Series **341**:303-307.

Cohen, J. 1988. Statistical power analysis for the behavioral sciences. 2nd edition. L. Erlbaum Associates, Hillsdale, N.J.

Coma, R., M. Ribes, J.-M. Gili, and M. Zabala. 2000. Seasonality in coastal benthic ecosystems. Trends in Ecology & Evolution **15**:448-453.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology **42**:710-723.

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. The American Naturalist **122**:661-696.

Cuddington, K. 2011. Legacy effects: the persistent impact of ecological interactions. Biological Theory **6**:203-210.

Cummins, S., D. Roberts, and K. Zimmerman. 2004. Effects of the green macroalga *Enteromorpha intestinalis* on macrobenthic and seagrass assemblages in a shallow coastal estuary. Marine Ecology Progress Series **266**:77-87.

Davis, B. C., and J. W. Fourqurean. 2001. Competition between the tropical alga, *Halimeda incrassata*, and the seagrass, *Thalassia testudinum*. Aquatic Botany **71**:217-232.

Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. Pages 81-96 *in* Proceedings of the Colloquium on Conservation Problems in Antarctica. Allen Press Lawrence, Kansas, USA.

de Fouw, J., Laura L. Govers, J. van de Koppel, J. van Belzen, W. Dorigo, Mohammed A. Sidi Cheikh, Marjolijn J. A. Christianen, Karin J. van der Reijden, M. van der Geest, T. Piersma, Alfons J. P. Smolders, H. Olff, Leon P. M. Lamers, Jan A. van Gils, and T. van der Heide. 2016. Drought, mutualism breakdown, and landscape-scale degradation of seagrass beds. Current Biology **26**:1051-1056.

Del Re, A. C. 2015. A practical tutorial on conducting meta-analysis in R. The Quantitative Methods for Psychology **11**:37-50.

Dennison, W. C., R. J. Orth, K. A. Moore, J. C. Stevenson, V. Carter, S. Kollar, P. W. Bergstrom, and R. A. Batiuk. 1993. Assessing water quality with submersed aquatic vegetation. BioScience **43**:86-94.

Dibble, E. D., S. M. Thomaz, and A. A. Padial. 2006. Spatial complexity measured at a multi-scale in three aquatic plant species. Journal of Freshwater Ecology **21**:239-247.

Dijkstra, J. A., J. Boudreau, and M. Dionne. 2012. Species-specific mediation of temperature and community interactions by multiple foundation species. Oikos **121**:646-654.

Duarte, C. M., and C. L. Chiscano. 1999. Seagrass biomass and production: a reassessment. Aquatic Botany **65**:159-174.

Duarte, C. M., J. J. Middelburg, and N. Caraco. 2005. Major role of marine vegetation on the oceanic carbon cycle. Biogeosciences **2**:1-8.

Dudley, T. L., S. D. Cooper, and N. Hemphill. 1986. Effects of macroalgae on a stream invertebrate community. Journal of the North American Benthological Society **5**:93-106.

Duval, S., and R. Tweedie. 2000. Trim and fill: a simple funnel-plot-based method of testing and adjusting for publication bias in meta-analysis. Biometrics **56**:455-463.

Egger, M., G. D. Smith, M. Schneider, and C. Minder. 1997. Bias in meta-analysis detected by a simple, graphical test. British Medical Journal **315**:629-634.
Eklöf, J. S., R. Henriksson, and N. Kautsky. 2006. Effects of tropical open-water seaweed farming on seagrass ecosystem structure and function. Marine Ecology Progress Series **325**:73-84.
Elder, J. F., and J. J. Collins. 1991. Freshwater molluscs as indicators of bioavailability and toxicity of metals in surface-water systems. Pages 37-79 *in* G. W. Ware, editor. Reviews of Environmental Contamination and Toxicology: Continuation of Residue Reviews. Springer New York, New York, NY.
Ellison, A. M., M. S. Bank, B. D. Clinton, E. A. Colburn, K. Elliott, C. R. Ford, D. R. Foster, B. D. Kloeppel, J. D. Knoepp, and G. M. Lovett. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment **3**:479-486.
Ellwood, M. D., and W. A. Foster. 2004. Doubling the estimate of invertebrate biomass in a rainforest canopy. Nature **429**:549.
Engelhardt, K. A., and M. E. Ritchie. 2001. Effects of macrophyte species richness on wetland ecosystem functioning and services. Nature **411**:687.
Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science **185**:1058-1060.
Everett, R. A. 1994. Macroalgae in marine soft-sediment communities: effects on benthic faunal assemblages. Journal of Experimental Marine Biology and Ecology **175**:253-274.
Folino-Rorem, N., J. Stoeckel, E. Thorn, and L. Page. 2006. Effects of artificial filamentous substrate on zebra mussel (*Dreissena polymorpha*) settlement. Biological Invasions **8**:89-96.
Fong, D. P., and D. J. B. Zedler. 2000. Sources, sinks, and fluxes of nutrients (N + P) in a small highly modified urban estuary in southern California. Urban Ecosystems **4**:125-144.
Fonseca, M. S., and J. A. Cahalan. 1992. A preliminary evaluation of wave attenuation by four species of seagrass. Estuarine, Coastal and Shelf Science **35**:565-576.
Fourqurean, J. W., C. M. Duarte, H. Kennedy, N. Marba, M. Holmer, M. A. Mateo, E. T. Apostolaki, G. A. Kendrick, D. Krause-Jensen, and K. J. McGlathery. 2012. Seagrass ecosystems as a globally significant carbon stock. Nature Geoscience **5**:505.
Fritz, K. M., M. M. Gangloff, and J. W. Feminella. 2004. Habitat modification by the stream macrophyte Justicia americana and its effects on biota. Oecologia **140**:388-397.
Gosling, E. 2008. Bivalve molluscs: biology, ecology and culture. John Wiley & Sons.
Grabowski, J. H., and C. H. Peterson. 2007. Restoring oyster reefs to recover ecosystem services. Pages 281-298 *in* C. K, B. JE, W. W, and H. A, editors. Ecosystem Engineers: Plants to Protists. Academic Press, New York, NY.
Graf, D. L., and K. S. Cummings. 2007. Review of the systematics and global diversity of freshwater mussel species (Bivalvia: Unionoida). Journal of Molluscan Studies **73**:291-314.
Gribben, P. E., J. E. Byers, J. T. Wright, and T. M. Glasby. 2013. Positive versus negative effects of an invasive ecosystem engineer on different components of a marine ecosystem. Oikos **122**:816-824.
Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. The American Naturalist **140**:539-572.
Gutiérrez, J. L., C. G. Jones, D. L. Strayer, and O. O. Iribarne. 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos **101**:79-90.
Guy-Haim, T., D. A. Lyons, J. Kotta, H. Ojaveer, A. M. Queirós, E. Chatzinikolaou, C. Arvanitidis, S. Como, P. Magni, A. J. Blight, H. Orav-Kotta, P. J. Somerfield, T. P. Crowe, and G. Rilov. 2018. Diverse effects of invasive ecosystem engineers on marine biodiversity and ecosystem functions: A global review and meta-analysis. Global Change Biology **24**:906-924.
Hallegraeff, G. M. 2010. Ocean climate change, phytoplankton community responses, and harmful algal blooms: a formidable predictive challenge. Journal of Phycology **46**:220-235.

Han, Q. Y., and D. Y. Liu. 2014. Macroalgae blooms and their effects on seagrass ecosystems. Journal of Ocean University of China **13**:791-798.

Harley, C. D. G., K. M. Anderson, K. W. Demes, J. P. Jorve, R. L. Kordas, T. A. Coyle, and M. H. Graham. 2012. Effects of climate change on global seaweed communities. Journal of Phycology **48**:1064-1078.

Harsch, M. A., P. E. Hulme, M. S. McGlone, and R. P. Duncan. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. Ecology Letters **12**:1040-1049.

He, H., X. Liu, X. Liu, J. Yu, K. Li, B. Guan, E. Jeppesen, and Z. Liu. 2014. Effects of cyanobacterial blooms on submerged macrophytes alleviated by the native Chinese bivalve *Hyriopsis cumingii*: A mesocosm experiment study. Ecological Engineering **71**:363-367.

Hedges, L. V. 1981. Distribution theory for Glass's estimator of effect size and related estimators. Journal of Educational Statistics **6**:107-128.

Heisler, J., P. M. Glibert, J. M. Burkholder, D. M. Anderson, W. Cochlan, W. C. Dennison, Q. Dortch, C. J. Gobler, C. A. Heil, E. Humphries, A. Lewitus, R. Magnien, H. G. Marshall, K. Sellner, D. A. Stockwell, D. K. Stoecker, and M. Suddleson. 2008. Eutrophication and harmful algal blooms: A scientific consensus. Harmful Algae **8**:3-13.

Hessing-Lewis, M. L., S. D. Hacker, B. A. Menge, and S. S. Rumrill. 2011. Context-dependent eelgrass–macroalgae interactions along an estuarine gradient in the Pacific Northwest, USA. Estuaries and Coasts **34**:1169-1181.

Higgins, S. N., and M. J. V. Zanden. 2010. What a difference a species makes: a meta–analysis of dreissenid mussel impacts on freshwater ecosystems. Ecological Monographs **80**:179-196.

Hoeksema, J. D., V. B. Chaudhary, C. A. Gehring, N. C. Johnson, J. Karst, R. T. Koide, A. Pringle, C. Zabinski, J. D. Bever, J. C. Moore, G. W. T. Wilson, J. N. Klironomos, and J. Umbanhowar. 2010. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. Ecology Letters **13**:394-407.

Holmer, M., P. Wirachwong, and M. S. Thomsen. 2011. Negative effects of stress-resistant drift algae and high temperature on a small ephemeral seagrass species. Marine Biology **158**:297-309.

Holmquist, J. 1994. Benthic macroalgae as a dispersal mechanism for fauna: influence of a marine tumbleweed. Journal of Experimental Marine Biology and Ecology **180**:235-251.

Hoyt, W. T., and A. C. Del Re. 2018. Effect size calculation in meta-analyses of psychotherapy outcome research. Psychotherapy Research **28**:379-388.

Hughes, A. R. R., K. J. Bando, L. F. Rodriguez, and S. L. Williams. 2004. Relative effects of grazers and nutrients on seagrasses: a meta-analysis approach. Marine Ecology Progress Series **282**.

Hurd, C. L., P. J. Harrison, K. Bischof, and C. S. Lobban. 2014. Seaweed ecology and physiology. Cambridge University Press.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs **54**:187-211.

Ilg, C., F. Dziock, F. Foeckler, K. Follner, M. Gerisch, J. Glaeser, A. Rink, A. Schanowski, M. Scholz, O. Deichner, and K. Henle. 2008. LONG-TERM REACTIONS OF PLANTS AND MACROINVERTEBRATES TO EXTREME FLOODS IN FLOODPLAIN GRASSLANDS. Ecology **89**:2392-2398.

Ingólfsson, A. 1995. Floating clumps of seaweed around Iceland: natural microcosms and a means of dispersal for shore fauna. Marine Biology **122**:13-21.

IPCC. 2007. Summary for Policymakers. Pages 1-18 *in* S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H. L. Miller, editors. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY.

Irlandi, E. 1996. The effects of seagrass patch size and energy regime on growth of a suspension-feeding bivalve. Journal of Marine Research **54**:161-185.

Irlandi, E. A. 1997. Seagrass patch size and survivorship of an infaunal bivalve. Oikos **78**:511-518.

Irlandi, E. A., W. G. Ambrose, and B. A. Orlando. 1995. Landscape ecology and the marine environment: how spatial configuration of seagrass habitat influences growth and survival of the bay scallop. Oikos **72**:307-313.
Jackson, J. K., and L. Füreder. 2006. Long-term studies of freshwater macroinvertebrates: a review of the frequency, duration and ecological significance. Freshwater Biology **51**:591-603.
Jenkins, S. R., and S. J. Hawkins. 2003. Barnacle larval supply to sheltered rocky shores: a limiting factor? Pages 143-151. Springer Netherlands, Dordrecht.
Kaenel, B. R., C. D. Matthaei, and U. Uehlinger. 1998. Disturbance by aquatic plant management in streams: Effects on benthic invertebrates. Regulated Rivers: Research & Management **14**:341-356.
Karatayev, A. Y., D. K. Padilla, D. Minchin, D. Boltovskoy, and L. E. Burlakova. 2007. Changes in global economies and trade: the potential spread of exotic freshwater bivalves. Biological Invasions **9**:161-180.
Kiirikki, M. 1996. Experimental evidence that *Fucus vesiculosus* (Phaeophyta) controls filamentous algae by means of the whiplash effect. European Journal of Phycology **31**:61-66.
Knox, G. A. 1986. Estuarine ecosystems: a systems approach. CRC Press, Boca Raton, Fla.
Kotta, J., K. Herkül, I. Kotta, H. Orav-Kotta, and V. Lauringson. 2009. Effects of the suspension feeding mussel *Mytilus trossulus* on a brackish water macroalgal and associated invertebrate community. Marine Ecology **30**:56-64.
Kumar, C. S., P. Ganesan, P. Suresh, and N. Bhaskar. 2008. Seaweeds as a source of nutritionally beneficial compounds-a review. Journal of Food Science and Technology **45**:1-13.
Lamote, M., and K. H. Dunton. 2006. Effects of drift macroalgae and light attenuation on chlorophyll fluorescence and sediment sulfides in the seagrass *Thalassia testudinum*. Journal of Experimental Marine Biology and Ecology **334**:174-186.
Larned, S. T. 2003. Effects of the invasive, nonindigenous seagrass *Zostera japonica* on nutrient fluxes between the water column and benthos in a NE Pacific estuary. Marine Ecology Progress Series **254**:69-80.
Leonard, G. H. 1999. Positive and negative effects of intertidal algal canopies on recruitment and survival of barnacles. Marine Ecology Progress Series **178**:241-249.
Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. Ecology Letters **7**:975-989.
Lilley, S. A., and D. R. Schiel. 2006. Community effects following the deletion of a habitat-forming alga from rocky marine shores. Oecologia **148**:672-681.
Limburg, K. E., V. A. Luzadis, M. Ramsey, K. L. Schulz, and C. M. Mayer. 2010. The good, the bad, and the algae: perceiving ecosystem services and disservices generated by zebra and quagga mussels. Journal of Great Lakes Research **36**:86-92.
López, M. S., and R. Coutinho. 2010. Positive interaction between the native macroalgae *Sargassum* sp. and the exotic bivalve *Isognomon bicolor*? Brazilian Journal of Oceanography **58**:69-72.
Lürling, M., G. van Geest, and M. Scheffer. 2006. Importance of nutrient competition and allelopathic effects in suppression of the green alga *Scenedesmus obliquus* by the macrophytes *Chara*, *Elodea* and *Myriophyllum*. Hydrobiologia **556**:209-220.
Lyons, D. A., C. Arvanitidis, A. J. Blight, E. Chatzinikolaou, T. Guy-Haim, J. Kotta, H. Orav-Kotta, A. M. Queirós, G. Rilov, and P. J. Somerfield. 2014. Macroalgal blooms alter community structure and primary productivity in marine ecosystems. Global Change Biology **20**:2712-2724.
Maciá, S. 2000. The effects of sea urchin grazing and drift algal blooms on a subtropical seagrass bed community. Journal of Experimental Marine Biology and Ecology **246**:53-67.
MacIsaac, H. J. 1994. Size-selective predation on zebra mussels (*Dreissena polymorpha*) by crayfish (*Orconectes propinquus*). Journal of the North American Benthological Society **13**:206-216.
MacIsaac, H. J. 1996. Potential abiotic and biotic impacts of zebra mussels on the inland waters of North America. American Zoologist **36**:287-299.

Magnuson, J. J. 1990. Long-term ecological research and the invisible present. BioScience **40**:495-501.
Markovic, D., S. F. Carrizo, O. Kärcher, A. Walz, and J. N. W. David. 2017. Vulnerability of European freshwater catchments to climate change. Global Change Biology **23**:3567-3580.
Marsden, I. D., and M. J. Bressington. 2009. Effects of macroalgal mats and hypoxia on burrowing depth of the New Zealand cockle (*Austrovenus stutchburyi*). Estuarine, Coastal and Shelf Science **81**:438-444.
Marsden, I. D., and S. R. Maclaren. 2010. Short-term study testing the resilience of an estuarine bivalve to macroalgal mats. Hydrobiologia **649**:217-229.
Martin, L. J., B. Blossey, and E. Ellis. 2012. Mapping where ecologists work: biases in the global distribution of terrestrial ecological observations. Frontiers in Ecology and the Environment **10**:195-201.
McGlathery, K. J. 2001. Macroalgal blooms contribute to the decline of seagrass in nutrient-enriched waters. Journal of Phycology **37**:453-456.
McMahon, K., C. Collier, and P. S. Lavery. 2013. Identifying robust bioindicators of light stress in seagrasses: A meta-analysis. Ecological Indicators **30**:7-15.
Montgomery, W. L., and S. D. Gerking. 1980. Marine macroalgae as foods for fishes: an evaluation of potential food quality. Environmental Biology of Fishes **5**:143-153.
Mouritsen, K. N. 2002. The parasite-induced surfacing behaviour in the cockle *Austrovenus stutchburyi*: a test of an alternative hypothesis and identification of potential mechanisms. Parasitology **124**.
Mundim, F. M., and E. M. Bruna. 2016. Is there a temperate bias in our understanding of how climate change will alter plant-herbivore interactions? A meta-analysis of experimental studies. The American Naturalist **188**:S74-S89.
Newell, R. I. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. Journal of Shellfish Research **23**:51-62.
Newell, R. I., and E. W. Koch. 2004. Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. Estuaries **27**:793-806.
Nikula, R., C. I. Fraser, H. G. Spencer, and J. M. Waters. 2010. Circumpolar dispersal by rafting in two subantarctic kelp-dwelling crustaceans. Marine Ecology Progress Series **405**:221-230.
Norkko, A., J. E. Hewitt, S. F. Thrush, and G. A. Funnell. 2006. Conditional outcomes of facilitation by a habitat-modifying subtidal bivalve. Ecology **87**:226-234.
Norkko, A., J. E. Hewitt, S. F. Thrush, and T. Funnell. 2001. Benthic-pelagic coupling and suspension-feeding bivalves: linking site-specific sediment flux and biodeposition to benthic community structure. Limnology and Oceanography **46**:2067-2072.
Norkko, J., E. Bonsdorff, and A. Norkko. 2000. Drifting algal mats as an alternative habitat for benthic invertebrates: Species specific responses to a transient resource. Journal of Experimental Marine Biology and Ecology **248**:79-104.
O'Connor, N. E., T. P. Crowe, and D. McGrath. 2006. Effects of epibiotic algae on the survival, biomass and recruitment of mussels, *Mytilus* L. (Bivalvia: Mollusca). Journal of Experimental Marine Biology and Ecology **328**:265-276.
Ólafsson, E., A. Ingólfsson, and M. B. Steinarsdóttir. 2001. Harpacticoid copepod communities of floating seaweed: controlling factors and implications for dispersal. Hydrobiologia **453**:189-200.
Orth, R. J. 1977. The importance of sediment stability in seagrass communities. Pages 281-300 *in* B. C. Coull, editor. Ecology of Marine Benthos. University of South Carolina Press, Columbia.
Orth, R. J., T. J. Carruthers, W. C. Dennison, C. M. Duarte, J. W. Fourqurean, K. L. Heck, A. R. Hughes, G. A. Kendrick, W. J. Kenworthy, and S. Olyarnik. 2006. A global crisis for seagrass ecosystems. BioScience **56**:987-996.

Orth, R. J., K. L. Heck, and J. van Montfrans. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries **7**:339-350.
Ozimek, T., E. Pieczyńska, and A. Hankiewicz. 1991. Effects of filamentous algae on submerged macrophyte growth: a laboratory experiment. Aquatic Botany **41**:309-315.
Peterson, B. J., and K. L. Heck Jr. 1999. The potential for suspension feeding bivalves to increase seagrass productivity. Journal of Experimental Marine Biology and Ecology **240**:37-52.
Peterson, B. J., and K. L. Heck Jr. 2001a. An experimental test of the mechanism by which suspension feeding bivalves elevate seagrass productivity. Marine Ecology Progress Series **218**:115-125.
Peterson, B. J., and K. L. Heck Jr. 2001b. Positive interactions between suspension-feeding bivalves and seagrass-a facultative mutualism. Marine Ecology Progress Series **213**:143-155.
Peterson, C. H. 1982. Clam predation by whelks (Busycon spp.): Experimental tests of the importance of prey size, prey density, and seagrass cover. Marine Biology **66**:159-170.
Pielou, E. C. 1977. The latitudinal spans of seaweed species and their patterns of overlap. Journal of Biogeography **4**:299-311.
Piola, R. F., and E. L. Johnston. 2008. Pollution reduces native diversity and increases invader dominance in marine hard-substrate communities. Diversity and Distributions **14**:329-342.
Platnick, N. I. 1991. Patterns of biodiversity: tropical vs temperate. Journal of Natural History **25**:1083-1088.
Posey, M. H., C. Wigand, and J. C. Stevenson. 1993. Effects of an introduced aquatic plant, *Hydrilla verticillata*, on benthic communities in the Upper Chesapeake Bay. Estuarine, Coastal and Shelf Science **37**:539-555.
Powell, E. N., and D. J. Davies. 1990. When is an "old" shell really old? The Journal of Geology **98**:823-844.
Powell, E. N., J. N. Kraeuter, and K. A. Ashton-Alcox. 2006. How long does oyster shell last on an oyster reef? Estuarine, Coastal and Shelf Science **69**:531-542.
Power, M. E. 1990. Benthic turfs vs floating mats of algae in river food webs. Oikos **58**:67-79.
Price, P. W. 1986. Parasite mediation in ecological interactions. Annual Review of Ecology and Systematics **17**:487-505.
Pyšek, P., D. M. Richardson, J. Pergl, V. Jarošík, Z. Sixtová, and E. Weber. 2008. Geographical and taxonomic biases in invasion ecology. Trends in Ecology & Evolution **23**:237-244.
Raffaelli, D. G., J. A. Raven, and L. J. Poole. 1998. Ecological impact of green macroalgal blooms. Oceanography and Marine Biology: an annual review **36**:97-125.
Rai, L. C., H. D. Kumar, F. H. Mohn, and C. J. Soeder. 2000. Services of algae to the environment. Journal of Microbiology and Biotechnology **10**:119-136.
Reusch, T., A. Chapman, and J. Groger. 1994. Blue mussels *Mytilus edulis* do not interfere with eelgrass *Zostera marina* but fertilize shoot growth through biodeposition. Marine Ecology Progress Series **108**:265-282.
Reusch, T. B., and S. L. Williams. 1998. Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia*. Oecologia **113**:428-441.
Reynolds, L. K., P. Berg, and J. C. Zieman. 2007. Lucinid clam influence on the biogeochemistry of the seagrass *Thalassia testudinum* sediments. Estuaries and Coasts **30**:482-490.
Ricciardi, A., F. G. Whoriskey, and J. B. Rasmussen. 1997. The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. Canadian Journal of Fisheries and Aquatic Sciences **54**:2596-2608.
Riginos, C., J. B. Grace, D. J. Augustine, and T. P. Young. 2009. Local versus landscape-scale effects of savanna trees on grasses. Journal of Ecology **97**:1337-1345.
Ripple, W. J., and R. L. Beschta. 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. Biological Conservation **145**:205-213.
Rothstein, H. R., A. J. Sutton, and M. Borenstein. 2006. Publication bias in meta-analysis: prevention, assessment and adjustments. John Wiley & Sons.

Rustad, L., J. Campbell, G. Marion, R. Norby, M. Mitchell, A. Hartley, J. Cornelissen, J. Gurevitch, and GCTE-NEWS. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia **126**:543-562.

Sand-Jensen, K. 1998. Influence of submerged macrophytes on sediment composition and near-bed flow in lowland streams. Freshwater Biology **39**:663-679.

Sanmartí, N., L. Solé, J. Romero, and M. Pérez. 2018. Seagrass-bivalve facilitative interactions: trait-mediated effects along an environmental gradient. Marine Environmental Research **133**:99-104.

Scheibling, R. E., and P. Gagnon. 2006. Competitive interactions between the invasive green alga *Codium fragile* ssp. *tomentosoides* and native canopy-forming seaweeds in Nova Scotia (Canada). Marine Ecology Progress Series **325**:1-14.

Scherner, F., P. A. Horta, E. C. de Oliveira, J. C. Simonassi, J. M. Hall-Spencer, F. Chow, J. M. C. Nunes, and S. M. B. Pereira. 2013. Coastal urbanization leads to remarkable seaweed species loss and community shifts along the SW Atlantic. Marine Pollution Bulletin **76**:106-115.

Schiel, D. R. 2011. Biogeographic patterns and long-term changes on New Zealand coastal reefs: Non-trophic cascades from diffuse and local impacts. Journal of Experimental Marine Biology and Ecology **400**:33-51.

Schiel, D. R., and S. A. Lilley. 2007. Gradients of disturbance to an algal canopy and the modification of an intertidal community. Marine Ecology Progress Series **339**:1-11.

Schmidt, A. L., M. Coll, T. N. Romanuk, and H. K. Lotze. 2011. Ecosystem structure and services in eelgrass *Zostera marina* and rockweed *Ascophyllum nodosum* habitats. Marine Ecology Progress Series **437**:51-68.

Schoener, T. W. 1983. Field experiments on interspecific competition. The American Naturalist **122**:240-285.

Schultz, R., and E. Dibble. 2012. Effects of invasive macrophytes on freshwater fish and macroinvertebrate communities: the role of invasive plant traits. Hydrobiologia **684**:1-14.

Schutten, J., J. Dainty, and A. J. Davy. 2005. Root anchorage and its significance for submerged plants in shallow lakes. Journal of Ecology **93**:556-571.

Semesi, I. S., S. Beer, and M. Björk. 2009. Seagrass photosynthesis controls rates of calcification and photosynthesis of calcareous macroalgae in a tropical seagrass meadow. Marine Ecology Progress Series **382**:41-47

Shili, A., E. B. Trabelsi, N. Ben Maïz, and C. Pergent-Martini. 2002. Benthic macrophyte communities in the Ghar El Melh lagoon (North Tunisia). Journal of Coastal Conservation **8**:135-140.

Sih, A. 1985. Predation, competition, and prey communities: a review of field experiments. Annual Review of Ecology and Systematics **16**:269-311.

Smith, K. A., E. W. North, F. Shi, S.-N. Chen, R. R. Hood, E. W. Koch, and R. I. Newell. 2009. Modeling the effects of oyster reefs and breakwaters on seagrass growth. Estuaries and Coasts **32**:748-757.

Sogard, S. M., and K. W. Able. 1991. A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. Estuarine, Coastal and Shelf Science **33**:501-519.

Stachowicz, J. J. 2001. Mutualism, facilitation, and the structure of ecological communities. BioScience **51**:235-246.

Strayer, D., J. S. Glitzenstein, C. G. Jones, J. Kolasa, G. E. Likens, M. J. McDonnell, G. G. Parker, and S. T. Pickett. 1986. Long-term ecological studies: an illustrated account of their design, operation, and importance to ecology. Occasional Publication of the Institute of Ecosystem Studies **2**.

Strayer, D. L., N. F. Caraco, J. J. Cole, S. Findlay, and M. L. Pace. 1999. Transformation of freshwater ecosystems by bivalves. BioScience **49**:19-27.

Taplin, K. A., E. A. Irlandi, and R. Raves. 2005. Interference between the macroalga *Caulerpa prolifera* and the seagrass *Halodule wrightii*. Aquatic Botany **83**:175-186.

Thiel, M., L. Stearns, and L. Watling. 1998. Effects of green algal mats on bivalves in a New England mud flat. Helgoländer Meeresuntersuchungen **52**:15-28.

Thiet, R. K., S. M. Smith, V. Rubino, R. Clark, K. Lee, and J. Oset. 2014. Soft shell clams (*Mya arenaria*) contribute to macroalgal blooms in a partially-restored Gulf of Maine back-barrier lagoon. Ecological Restoration **32**:46-58.

Thompson, R. M., J. Beardall, J. Beringer, M. Grace, and P. Sardina. 2013. Means and extremes: building variability into community-level climate change experiments. Ecology Letters **16**:799-806.

Thompson, S. G., and S. J. Sharp. 1999. Explaining heterogeneity in meta-analysis: a comparison of methods. Statistics in Medicine **18**:2693-2708.

Thomsen, M., P. Stæhr, L. Nejrup, and D. Schiel. 2013. Effects of the invasive macroalgae *Gracilaria vermiculophylla* on two co-occurring foundation species and associated invertebrates. Aquatic Invasions **8**:133-145.

Thomsen, M., T. Wernberg, J. Olden, J. E. Byers, J. Bruno, B. Silliman, and D. Schiel. 2014. Forty years of experiments on aquatic invasive species: are study biases limiting our understanding of impacts? NeoBiota **22**.

Thomsen, M. S., A. H. Altieri, C. Angelini, M. J. Bishop, P. E. Gribben, G. Lear, Q. He, D. R. Schiel, B. R. Silliman, P. M. South, D. M. Watson, T. Wernberg, and G. Zotz. 2018. Secondary foundation species enhance biodiversity. Nature Ecology & Evolution **2**:634-639.

Thomsen, M. S., T. de Bettignies, T. Wernberg, M. Holmer, and B. Debeuf. 2012a. Harmful algae are not harmful to everyone. Harmful Algae **16**:74-80.

Thomsen, M. S., T. Hildebrand, P. M. South, T. Foster, A. Siciliano, E. Oldach, and D. R. Schiel. 2016. A sixth-level habitat cascade increases biodiversity in an intertidal estuary. Ecology and evolution **6**:8291-8303.

Thomsen, M. S., T. Wernberg, A. Altieri, F. Tuya, D. Gulbransen, K. J. McGlathery, M. Holmer, and B. R. Silliman. 2010. Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. Integrative and Comparative Biology **50**:158-175.

Thomsen, M. S., T. Wernberg, A. H. Engelen, F. Tuya, M. A. Vanderklift, M. Holmer, K. J. McGlathery, F. Arenas, J. Kotta, and B. R. Silliman. 2012b. A meta-analysis of seaweed impacts on seagrasses: generalities and knowledge gaps. PLoS One **7**:1-8.

Thomsen, M. S., T. Wernberg, F. Tuya, and B. R. Silliman. 2009. Evidence for impacts of nonindigenous macroalgae: a meta-analysis of experimental field studies. Journal of Phycology **45**:812-819.

Tilman, D. 1989. Ecological experimentation: strengths and conceptual problems. Pages 136-157 *in* G. E. Likens, editor. Long-term studies in ecology. Springer-Verlag, New York.

Tirado, R., and F. I. Pugnaire. 2005. Community structure and positive interactions in constraining environments. Oikos **111**:437-444.

Tolley, S. G., and A. K. Volety. 2005. The role of oysters in habitat use of oyster reefs by resident fishes and decapod crustaceans. Journal of Shellfish Research **24**:1007-1012.

Trimble, M. J., and R. J. van Aarde. 2012. Geographical and taxonomic biases in research on biodiversity in human-modified landscapes. Ecosphere **3**:1-16.

Turner, M. G., S. L. Collins, A. L. Lugo, J. J. Magnuson, T. S. Rupp, and F. J. Swanson. 2003. Disturbance dynamics and ecological response: the contribution of long-term ecological research. BioScience **53**:46-56.

Valiela, I., J. McClelland, J. Hauxwell, P. J. Behr, D. Hersh, and K. Foreman. 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnology and Oceanography **42**:1105-1118.

van der Heide, T., L. L. Govers, J. de Fouw, H. Olff, M. van der Geest, M. M. van Katwijk, T. Piersma, J. van de Koppel, B. R. Silliman, A. J. Smolders, and J. A. van Gills. 2012. A three-stage symbiosis forms the foundation of seagrass ecosystems. Science **336**:1432-1434.

Vázquez, G., P. Moreno-Casasola, and O. Barrera. 1998. Interaction between algae and seed germination in tropical dune slack species: a facilitation process. Aquatic Botany **60**:409-416.

Villegas, M. J., J. Laudien, W. Sielfeld, and W. E. Arntz. 2008. *Macrocystis integrifolia* and *Lessonia trabeculata* (Laminariales; Phaeophyceae) kelp habitat structures and associated macrobenthic community off northern Chile. Helgoland Marine Research **62**:33-43.

Wahl, M. 1997. Increased drag reduces growth of snails: comparison of flume and in situ experiments. Marine Ecology Progress Series **151**:291-293.

Wahl, M. 2008. Ecological lever and interface ecology: epibiosis modulates the interactions between host and environment. Biofouling **24**:427-438.

Walker, D. I., B. Olesen, and R. C. Phillips. 2001. Reproduction and phenology in seagrasses. Pages 59-78 *in* F. T. Short and R. G. Coles, editors. Global Seagrass Research Methods. Elsevier.

Wall, C. C., B. J. Peterson, and C. J. Gobler. 2008. Facilitation of seagrass *Zostera marina* productivity by suspension-feeding bivalves. Marine Ecology Progress Series **357**:165-174.

Ward, J. M., and A. Ricciardi. 2007. Impacts of *Dreissena* invasions on benthic macroinvertebrate communities: a meta-analysis. Diversity and Distributions **13**:155-165.

Ward, J. M., and A. Ricciardi. 2010. Community-level effects of co-occurring native and exotic ecosystem engineers. Freshwater Biology **55**:1803-1817.

Watson, D. M., and M. Herring. 2012. Mistletoe as a keystone resource: an experimental test. Proceedings of the Royal Society of London B: Biological Sciences **279**:3853-3860.

Williams, S. L., and K. L. Heck Jr. 2001. Seagrass community ecology. Pages 317-337 *in* M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. Marine community ecology. Sinauer Associates, Sunderland, MA.

Wilson, J. R. U., S. Proches, B. Braschler, E. S. Dixon, and D. M. Richardson. 2007. The (bio)diversity of science reflects the interests of society. Frontiers in Ecology and the Environment **5**:409-414.

Witman, J. D., and T. H. Suchanek. 1984. Mussels in flow: drag and dislodgement by epizoans. Marine Ecology Progress Series **16**:259-268.

Woodward, G., D. M. Perkins, and L. E. Brown. 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. Philosophical Transactions of the Royal Society B: Biological Sciences **365**:2093-2106.

Young, A., and N. Mitchell. 1994. Microclimate and vegetation edge effects in a fragmented podocarp-broadleaf forest in New Zealand. Biological Conservation **67**:63-72.

Zu Ermgassen, P. S., M. D. Spalding, R. E. Grizzle, and R. D. Brumbaugh. 2013. Quantifying the loss of a marine ecosystem service: filtration by the eastern oyster in US estuaries. Estuaries and Coasts **36**:36-43.

Supplementary material

Supporting tables and figures

Table S1. Types of performance responses found in the 242 interactions extracted for meta-analysis. Foundation species at the top row are the dependent variable. Each performance response was put into a general category with similar interactions; the abundance category included measurements of biomass, density, or coverage. The size category consisted of length measurements. Processes included elements such as recruitment, production, and survival. The category of 'other' was for studies that measured anything outside of the three categories. *n* is the number of studies included in each category, and % is the ratio of each category to the total number of studies for a foundation species.

	Angiosperm		**Algae**		**Bivalve**	
Variable	*n*	%	*n*	%	*n*	%
Abundance	54	41.2	17	58.6	29	35.4
Size	18	13.7	4	13.8	10	12.2
Processes	56	42.8	4	13.8	38	46.3
Other	3	2.3	4	13.8	5	6.1
Total	**131**		**29**		**82**	

Figure S1. Funnel plot of standard error by Hedge's *g* of all interactions. Filled circles are publications used in this meta-analysis (one large effect size *g*=39.2, was removed for ease of visualization), while open circles indicate missing studies assuming symmetry. The trim-and-fill method found 49 missing studies on the right side of the plot, indicating publication bias. The Egger's regression also found funnel plot asymmetry ($p<0.001$), indicating that there was publication bias.

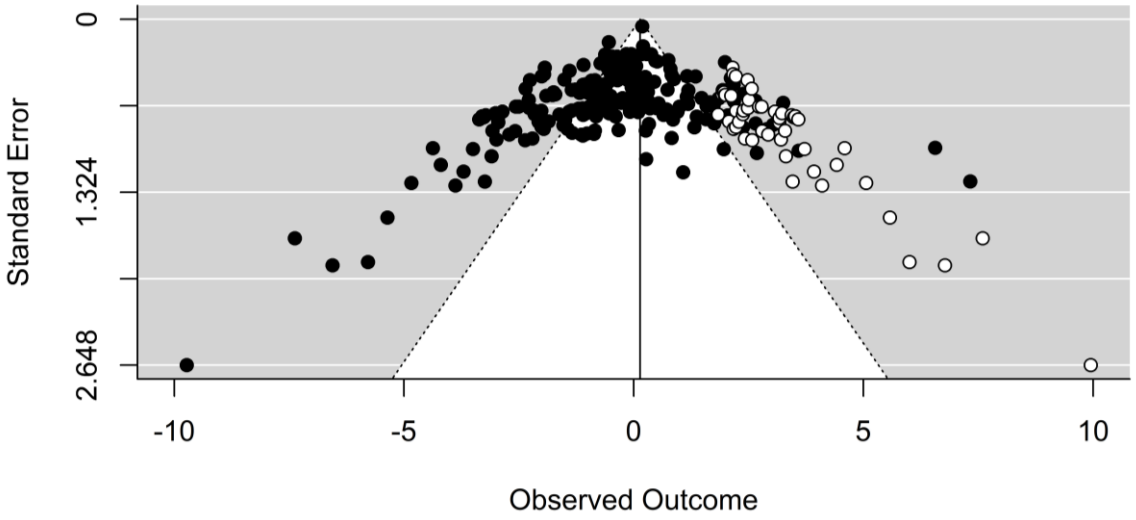


Figure S2. Funnel plot of standard error by Hedge's *g* for angiosperm interactions. Filled circles are publications used in this meta-analysis, while open circles indicate missing studies. The trim-and-fill method found 3 missing studies on the left side of the plot, indicating

publication bias. The Egger's regression also found funnel plot asymmetry (p=0.019), indicating that there was publication bias.

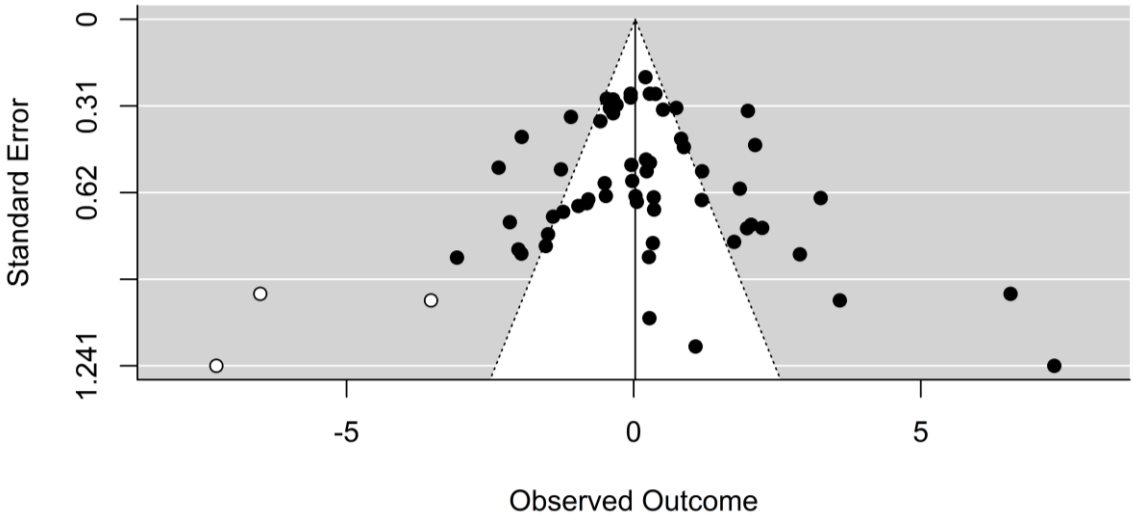


Figure S3. Funnel plot of standard error by Hedge's *g* for macroalgae interactions. Filled circles are publications used in this meta-analysis, while open circles indicate missing studies. The trim-and-fill method found 5 missing studies on the right side of the plot, indicating publication bias. The Egger's regression also found funnel plot asymmetry (p<0.001), indicating that there was publication bias.

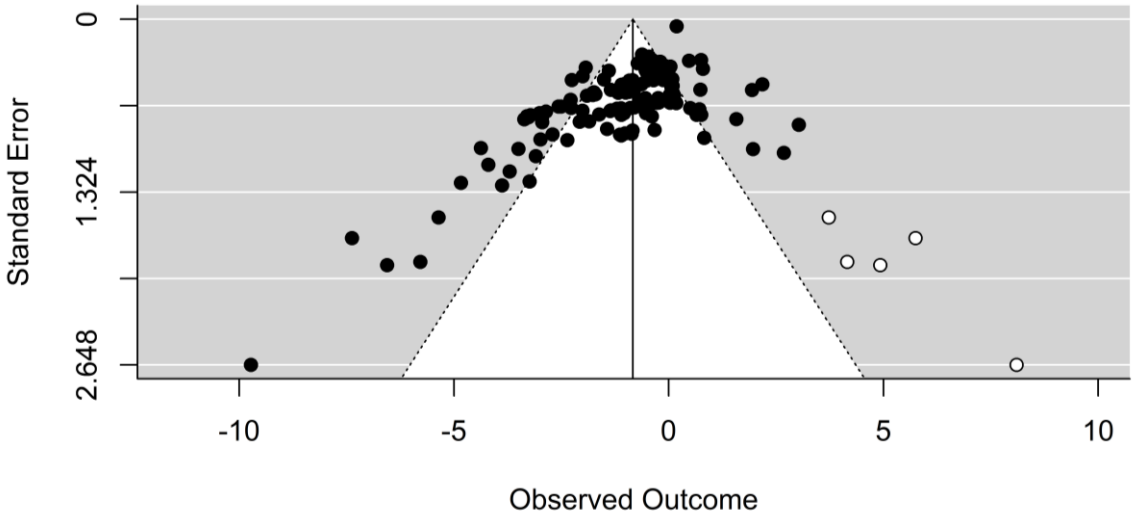
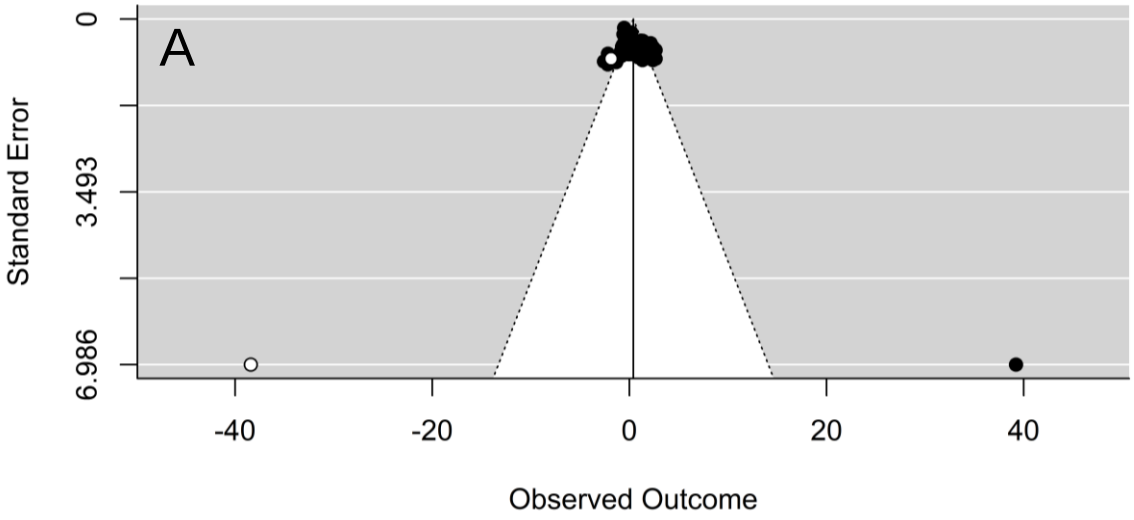
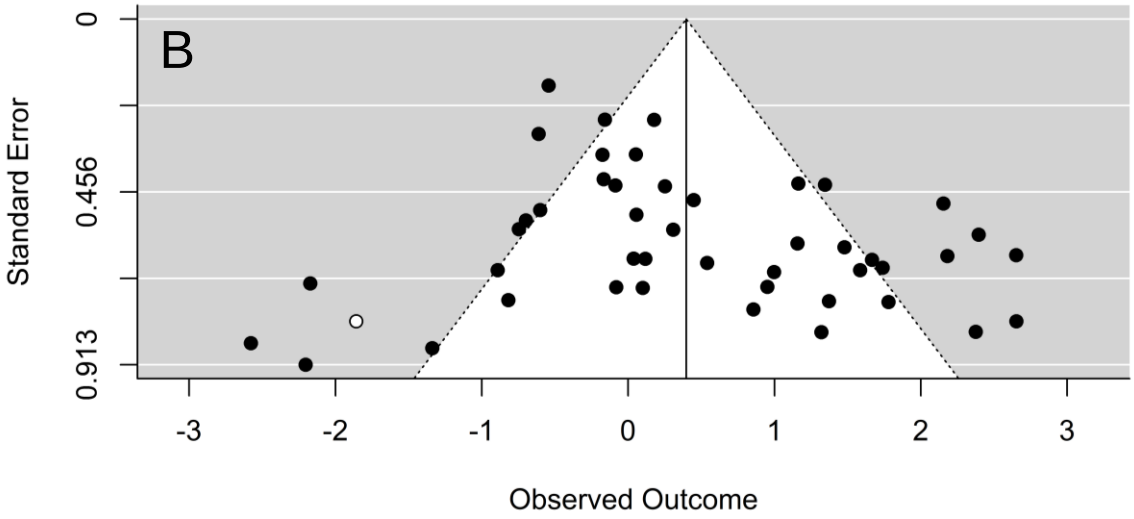


Figure S4. (A) Funnel plot of standard error by Hedge's *g* for bivalve interactions. Filled circles are publications used in this meta-analysis, while open circles indicate missing studies. The trim-and-fill method found 2 missing studies on the left side of the plot, indicating publication bias. The Egger's regression also found funnel plot asymmetry (p<0.001), indicating that there was publication bias. (B) Funnel plot with the large effect size removed (39.2). The trim-and-fill method found 1 missing study on the left side of the plot, but otherwise the funnel plot seems approximately symmetrical, the Egger's regression showed no significant publication bias (p=0.495).


A
Standard Error
0
3.493
6.986
-40
-20
0
20
40
Observed Outcome


B
Standard Error
0
0.456
0.913
-3
-2
-1
0
1
2
3
Observed Outcome

Statistical results

Explanatory variable 1: FS interactions (Figure 4A)

Model summary:

	Estimate	SE	Z	95% CI		p
Intercept	-1.119	0.142	-7.907	-1.396	-0.842	<0.001
Macroalgae→Bivalve	0.629	0.248	2.535	0.143	1.116	0.011
Angiosperm→Macroalgae	0.945	0.332	2.847	0.294	1.596	0.004
Angiosperm→Bivalve	1.541	0.253	6.089	1.045	2.036	<0.001
Bivalve→Macroalgae	1.415	0.442	3.198	0.548	2.282	0.001
Bivalve→Angiosperm	1.642	0.266	6.179	1.121	2.163	<0.001

Heterogeneity and model-fit:

QE	QE df	QE p	QM	QM df	QM p
1176.99	236	0	61.299	5	<0.001

	Estimate	95% CI	
tau^2	1.41	1.66	2.94
tau	1.19	1.29	1.71
I^2 (%)	86.24	88.09	92.89
H^2	7.27	8.40	14.07

Subgroup Models

Subgroup	N	Estimate	95% CI		SE	p
Angiosperm→Macroalgae	19	-0.183	-0.675	0.309	0.251	0.466
Angiosperm→Bivalve	41	0.462	-0.096	1.020	0.285	0.105
Macroalgae→Angiosperm	95	-1.127	-1.142	-0.842	0.145	<0.001
Macroalgae→Bivalve	41	-0.471	-0.760	-0.182	0.148	0.001
Bivalve→Macroalgae	36	0.524	0.095	0.953	0.219	0.017
Bivalve→ Angiosperm	10	0.092	-0.273	0.458	0.187	0.621

Explanatory variable 2: FS size interactions (Figure 4B)

Model summary:

	Estimate	SE	Z	95% CI		p
Intercept	-0.786	0.175	-4.504	-1.128	-0.444	<0.001
Macroalgae→Medium	0.059	0.271	0.219	-0.471	0.590	0.826
Macroalgae→Small	-0.643	0.299	-2.146	-1.229	-0.056	0.032
Angiosperm→Large	1.660	0.728	2.281	0.234	3.086	0.023
Angiosperm→Medium	1.040	0.274	3.800	0.504	1.577	<0.001
Angiosperm→Small	0.801	0.378	2.121	0.061	1.542	0.034
Bivalve→Large	1.309	0.297	4.400	0.726	1.891	<0.001
Bivalve→Medium	1.386	0.442	3.133	0.519	2.254	0.002
Bivalve→Small	0.384	0.754	0.509	-1.094	1.863	0.611

Heterogeneity and model-fit:

QE	QE df	QE p	QM	QM df	QM p
1143.891	233	0	60.218	8	<0.001

	Estimate	95% CI	
tau^2	1.43	1.70	3.02
tau	1.20	1.31	1.74
I^2 (%)	86.15	88.11	92.94
H^2	7.22	8.41	14.15

Subgroup Models:

Subgroup	N	Estimate	95% CI		SE	p
Angiosperm→Small	16	-0.009	-0.819	0.800	0.413	0.982
Angiosperm→Medium	40	0.264	-0.172	0.699	0.222	0.236
Angiosperm→Large	4	1.105	-2.411	4.621	1.794	0.538
Macroalgae→Small	30	-1.444	-1.955	-0.933	0.261	<0.001
Macroalgae→Medium	46	-0.761	-1.209	-0.314	0.228	0.001
Macroalgae→Large	60	-0.680	-0.892	-0.468	0.108	<0.001
Bivalve→Small	3	-0.501	-0.812	-0.190	0.159	0.002
Bivalve→Medium	11	0.484	-0.121	1.088	0.308	0.117
Bivalve→Large	32	0.525	0.070	0.980	0.232	0.024

Explanatory variable 3: Experiment type (Figure 4C)

Model summary:

	Estimate	SE	Z	95% CI		p
Intercept	-0.573	0.140	-4.083	-0.848	-0.298	<0.001
Macroalgae Lab	-0.984	0.240	-4.102	-1.454	-0.514	<0.001
Angiosperm Field	0.782	0.227	3.446	0.337	1.228	0.001
Angiosperm Lab	0.907	0.520	1.743	-0.113	1.926	0.081
Bivalve Field	0.889	0.261	3.410	0.378	1.399	0.001
Bivalve Lab	1.592	0.436	3.647	0.736	2.447	<0.001

Heterogeneity and model-fit:

QE	QE df	QE p	QM	QM df	QM p
1170.668	236	<0.001	72.826	5	<0.001

	Estimate	95% CI	
tau^2	1.33	1.58	2.81

tau	1.16	1.26	1.68
I^2 (%)	86.37	88.26	93.02
H^2	7.34	8.51	14.34

Subgroup	N	Estimate	95% CI		SE	p
Angiosperm Field	54	0.247	-0.219	0.713	0.238	0.300
Angiosperm Lab	6	0.269	0.001	0.537	0.137	0.049
Macroalgae Field	85	-0.541	-0.753	-0.329	0.108	<0.001
Macroalgae Lab	51	-1.597	-2.026	-1.167	0.219	<0.001
Bivalve Field	34	0.314	-0.057	0.686	0.190	0.098
Bivalve Lab	12	1.044	0.139	1.950	0.462	0.024

Explanatory variable 4: Ecosystem type (Figure 4D)

	Estimate	SE	Z	95% CI		p
Intercept	-0.911	0.443	-2.057	-1.779	-0.043	0.040
Macroalgae Marine	-0.009	0.460	-0.019	-0.910	0.892	0.985
Angiosperm Freshwater	0.931	0.668	1.393	-0.379	2.241	0.164
Angiosperm Marine	1.169	0.481	2.431	0.227	2.112	0.015
Bivalve Freshwater	1.222	0.901	1.357	-0.543	2.988	0.175
Bivalve Marine	1.396	0.490	2.850	0.436	2.357	0.004

QE	QE df	QE p	QM	QM df	QM p
1293.118	236	<0.001	50.771	5	<0.001

	Estimate	95% CI	
tau^2	1.48	1.74	3.07
tau	1.22	1.32	1.75
I^2 (%)	87.64	89.30	93.63
H^2	8.09	9.35	15.70

Subgroup	N	Estimate	95% CI		SE	p
Angiosperm Marine	53	0.290	-0.177	0.756	0.238	0.223
Angiosperm Fresh	7	0.144	-0.311	0.539	0.217	0.598
Macroalgae Marine	126	-0.893	-1.109	-0.678	0.110	<0.001
Macroalgae Fresh	10	-1.016	-2.189	0.156	0.598	0.089
Bivalve Marine	43	0.476	0.108	0.850	0.189	0.011
Bivalve Fresh	3	0.227	-0.915	1.369	0.583	0.696

Explanatory variable 5: Latitude (Figure 5A)

Model summary:

	Estimate	SE	Z	95% CI		p
Intercept	-0.578	0.336	-1.724	-1.236	0.079	0.085
Latitude	0.005	0.008	0.648	-0.011	0.021	0.517

Regression model equation: -0.578 + 0.005*Latitude

Heterogeneity and model-fit:

QE	QE df	QE p	QM	QM df	QM p
1335.45	240	0	0.42	1	0.517

	Estimate	95% CI	
tau^2	1.84	2.16	3.73
tau	1.36	1.47	1.93
I^2 (%)	90.33	91.65	94.98
H^2	10.34	11.97	19.91

Explanatory variable 6: Experiment length (Figure 5B)

Model summary:

	Estimate	SE	Z	95% CI		p
Intercept	-0.346	0.116	-2.967	-0.574	-0.117	0.003
Exp. Length	-0.005	0.014	-0.383	-0.033	0.022	0.702

Regression model equation: -0.346 + -0.005*Exp. Length

Heterogeneity and model-fit:

QE	QE df	QE p	QM	QM df	QM p
1330.428	240	0	0.146	1	0.702

	Estimate	95% CI	
tau^2	1.85	2.17	3.73
tau	1.36	1.47	1.93
I^2 (%)	90.14	91.47	94.87
H^2	10.14	11.72	19.48

List of retained publications

Allen, B. J., and Williams, S. L. 2003. Native eelgrass *Zostera marina* controls growth and reproduction of an invasive mussel through food limitation. Marine Ecology Progress Series **254**:57-67.

Auffrey, L. M., Robinson, S. M., and Barbeau, M. A. 2004. Effect of green macroalgal mats on burial depth of soft-shelled clams *Mya arenaria*. Marine Ecology Progress Series **278**:193-203.

Booth, D. M., and Heck Jr., K. L. 2009. Effects of the American oyster *Crassostrea virginica* on growth rates of the seagrass *Halodule wrightii*. Marine Ecology Progress Series **389**:117-126.

Boström, C., and Bonsdorff, E. 2000. Zoobenthic community establishment and habitat complexity the importance of seagrass shoot-density, morphology and physical disturbance for faunal recruitment. Marine Ecology Progress Series **205**:123-138.

Brun, F. G., Hernández, I., Vergara, J. J., and Pérez-Lloréns, J. L. 2003a. Growth, carbon allocation and proteolytic activity in the seagrass *Zostera noltii* shaded by *Ulva* canopies. Functional Plant Biology **30**:551-560.

Brun, F. G., Vergara, J. J., Navarro, G., Hernández, I., and Pérez-Lloréns, J. L. 2003b. Effect of shading by *Ulva rigida* canopies on growth and carbon balance of the seagrass *Zostera noltii*. Marine Ecology Progress Series **265**:85-96.

Brun, F. G., Zetten, E., Cacabelos, E., and Bouma, T. J. 2009. Role of two contrasting ecosystem engineers (*Zostera noltii* and *Cymodocea nodosa*) on the food intake rate of *Cerastoderma edule*. Helgoland Marine Research **63**:19-25.

Carroll, J., Gobler, C. J., and Peterson, B. J. 2008. Resource-restricted growth of eelgrass in New York estuaries: Light limitation, and alleviation of nutrient stress by hard clams. Marine Ecology Progress Series **369**:51-62.

Carroll, J. M., Peterson, B. J., Bonal, D., Weinstock, A., Smith, C. F., and Tettelbach, S. T. 2010. Comparative survival of bay scallops in eelgrass and the introduced alga, *Codium fragile*, in a New York estuary. Marine Biology **157**:249-259.

Ceccherelli, G., and Campo, D. 2002. Different effects of *Caulerpa racemosa* on two co-occurring seagrasses in the Mediterranean. Page 71 Botanica Marina.

Ceccherelli, G., and Cinelli, F. 1997. Short-term effects of nutrient enrichment of the sediment and interactions between the seagrass *Cymodocea nodosa* and the introduced green alga *Caulerpa taxifolia* in a Mediterranean bay. Journal of Experimental Marine Biology and Ecology **217**:165-177.

Ceccherelli, G., and Cinelli, F. 1999. Effects of *Posidonia oceanica* canopy on *Caulerpa taxifolia* size in a north-western Mediterranean bay. Journal of Experimental Marine Biology and Ecology **240**:19-36.

Ceccherelli, G., Piazzi, L., and Cinelli, F. 2000. Response of the non-indigenous *Caulerpa racemosa* (Forsskål) J. Agardh to the native seagrass *Posidonia oceanica* (L.) Delile: effect of density of shoots and orientation of edges of meadows. Journal of Experimental Marine Biology and Ecology **243**:227-240.

Ceccherelli, G., and Sechi, N. 2002. Nutrient availability in the sediment and the reciprocal effects between the native seagrass *Cymodocea nodosa* and the introduced rhizophytic alga *Caulerpa taxifolia*. Hydrobiologia **474**:57-66.

Coen, L. D., and Heck Jr., K. L. 1991. The interacting effects of siphon nipping and habitat on bivalve (*Mercenaria mercenaria* (L.)) growth in a subtropical seagrass (*Halodule wrightii* Aschers) meadow. Journal of Experimental Marine Biology and Ecology **145**:1-13.

Cummins, S., Roberts, D., and Zimmerman, K. 2004. Effects of the green macroalga *Enteromorpha intestinalis* on macrobenthic and seagrass assemblages in a shallow coastal estuary. Marine Ecology Progress Series **266**:77-87.

Davis, B. C., and Fourqurean, J. W. 2001. Competition between the tropical alga, *Halimeda incrassata*, and the seagrass, *Thalassia testudinum*. Aquatic Botany **71**:217-232.

Deegan, L. A., Wright, A., Ayvazian, S. G., Finn, J. T., Golden, H., Merson, R. R., and Harrison, J. 2002. Nitrogen loading alters seagrass ecosystem structure and support of higher trophic levels. Aquatic Conservation-Marine and Freshwater Ecosystems **12**:193-212.

Dobretsov, S. V. 1999. Effects of macroalgae and biofilm on settlement of blue mussel (*Mytilus edulis* L.) larvae. Biofouling **14**:153-165.

Drouin, A., McKindsey, C. W., and Johnson, L. E. 2011. Higher abundance and diversity in faunal assemblages with the invasion of *Codium fragile* ssp. *fragile* in eelgrass meadows. Marine Ecology Progress Series **424**:105-117.

Eklöf, J. S., Henriksson, R., and Kautsky, N. 2006. Effects of tropical open-water seaweed farming on seagrass ecosystem structure and function. Marine Ecology Progress Series **325**:73-84.

Everett, R. A. 1991. Intertidal distribution of infauna in a central California lagoon: The role of seasonal blooms of macroalgae. Journal of Experimental Marine Biology and Ecology **150**:223-247.

Everett, R. A. 1994. Macroalgae in marine soft-sediment communities: Effects on benthic faunal assemblages. Journal of Experimental Marine Biology and Ecology **175**:253-274.

Folino-Rorem, N., Stoeckel, J., Thorn, E., and Page, L. 2006. Effects of artificial filamentous substrate on zebra mussel (*Dreissena polymorpha*) settlement. Biological Invasions **8**:89-96.

Fritz, K. M., Gangloff, M. M., and Feminella, J. W. 2004. Habitat modification by the stream macrophyte *Justicia americana* and its effects on biota. Oecologia **140**:388-397.

Garner, Y. L., and Litvaitis, M. K. 2013. Effects of wave exposure, temperature and epibiont fouling on byssal thread production and growth in the blue mussel, *Mytilus edulis*, in the Gulf of Maine. Journal of Experimental Marine Biology and Ecology **446**:52-56.

Gribben, P. E., Byers, J. E., Clements, M., McKenzie, L. A., Steinberg, P. D., and Wright, J. T. 2009. Behavioural interactions between ecosystem engineers control community species richness. Ecol Lett **12**:1127-1136.

Gribben, P. E., Byers, J. E., Wright, J. T., and Glasby, T. M. 2013. Positive versus negative effects of an invasive ecosystem engineer on different components of a marine ecosystem. Oikos **122**:816-824.

Hauxwell, J., Cebrián, J., Furlong, C., and Valiela, I. 2001. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. Ecology **82**:1007-1022.

He, H., Liu, X., Liu, X., Yu, J., Li, K., Guan, B., Jeppesen, E., and Liu, Z. 2014. Effects of cyanobacterial blooms on submerged macrophytes alleviated by the native Chinese bivalve *Hyriopsis cumingii*: A mesocosm experiment study. Ecological Engineering **71**:363-367.

Hessing-Lewis, M. L., Hacker, S. D., Menge, B. A., and Rumrill, S. S. 2011. Context-dependent eelgrass–macroalgae interactions along an estuarine gradient in the Pacific Northwest, USA. Estuaries and Coasts **34**:1169-1181.

Höffle, H., Thomsen, M. S., and Holmer, M. 2011. High mortality of *Zostera marina* under high temperature regimes but minor effects of the invasive macroalgae *Gracilaria vermiculophylla*. Estuarine, Coastal and Shelf Science **92**:35-46.

Holmer, M., and Nielsen, R. M. 2007. Effects of filamentous algal mats on sulfide invasion in eelgrass (*Zostera marina*). Journal of Experimental Marine Biology and Ecology **353**:245-252.

Holmer, M., Wirachwong, P., and Thomsen, M. S. 2011. Negative effects of stress-resistant drift algae and high temperature on a small ephemeral seagrass species. Marine Biology **158**:297-309.

Huntington, B. E., and Boyer, K. E. 2008. Effects of red macroalgal (*Gracilariopsis* sp.) abundance on eelgrass *Zostera marina* in Tomales Bay, California, USA. Marine Ecology Progress Series **367**:133-142.

Irlandi, E. 1994. Large-and small-scale effects of habitat structure on rates of predation: How percent coverage of seagrass affects rates of predation and siphon nipping on an infaunal bivalve. Oecologia **98**:176-183.

Irlandi, E. 1996. The effects of seagrass patch size and energy regime on growth of a suspension-feeding bivalve. Journal of Marine Research **54**:161-185.
Irlandi, E., Orlando, B., and Biber, P. 2004. Drift algae-epiphyte-seagrass interactions in a subtropical *Thalassia testudinum* meadow. Marine Ecology Progress Series **279**:81-91.
Irlandi, E. A. 1997. Seagrass patch size and survivorship of an infaunal bivalve. Oikos **78**:511-518.
Irlandi, E. A., Ambrose, W. G., and Orlando, B. A. 1995. Landscape ecology and the marine environment: How spatial configuration of seagrass habitat influences growth and survival of the bay scallop. Oikos **72**:307-313.
Irlandi, E. A., and Peterson, C. H. 1991. Modification of animal habitat by large plants: Mechanisms by which seagrasses influence clam growth. Oecologia **87**:307-318.
Kaenel, B. R., Matthaei, C. D., and Uehlinger, U. 1998. Disturbance by aquatic plant management in streams: Effects on benthic invertebrates. Regulated Rivers: Research & Management **14**:341-356.
Kotta, J., Herkül, K., Kotta, I., Orav-Kotta, H., and Lauringson, V. 2009. Effects of the suspension feeding mussel *Mytilus trossulus* on a brackish water macroalgal and associated invertebrate community. Marine Ecology **30**:56-64.
Lamote, M., and Dunton, K. H. 2006. Effects of drift macroalgae and light attenuation on chlorophyll fluorescence and sediment sulfides in the seagrass *Thalassia testudinum*. Journal of Experimental Marine Biology and Ecology **334**:174-186.
Maciá, S. 2000. The effects of sea urchin grazing and drift algal blooms on a subtropical seagrass bed community. Journal of Experimental Marine Biology and Ecology **246**:53-67.
MacIsaac, H. J. 1994. Size-selective predation on zebra mussels (*Dreissena polymorpha*) by crayfish (*Orconectes propinquus*). Journal of the North American Benthological Society **13**:206-216.
Marsden, I. D., and Maclaren, S. R. 2010. Short-term study testing the resilience of an estuarine bivalve to macroalgal mats. Hydrobiologia **649**:217-229.
Martínez-Lüscher, J., and Holmer, M. 2010. Potential effects of the invasive species *Gracilaria vermiculophylla* on *Zostera marina* metabolism and survival. Marine Environmental Research **69**:345-349.
Moreno-Marín, F., Vergara, J. J., Pérez-Llorens, J. L., Pedersen, M. F., and Brun, F. G. 2016. Interaction between ammonium toxicity and green tide development over seagrass meadows: A laboratory study. PLoS One **11**:1-17.
Msuya, F., and Salum, D. 2011. Effect of the presence of seagrass and nutrients on growth rates of farmed *Kappaphycus alvarezii* and *Eucheuma denticulatum* (rhodophyta). Western Indian Ocean Journal of Marine Science **10**:129.
Nakaoka, M. 2000. Nonlethal effects of predators on prey populations: predator-mediated change in bivalve growth. Ecology **81**:1031-1045.
Nelson, T. A., and Lee, A. 2001. A manipulative experiment demonstrates that blooms of the macroalga *Ulvaria obscura* can reduce eelgrass shoot density. Aquatic Botany **71**:149-154.
Norderhaug, K. M., Christie, H., and Fredriksen, S. 2007. Is habitat size an important factor for faunal abundances on kelp (*Laminaria hyperborea*)? Journal of Sea Research **58**:120-124.
Norkko, A., and Bonsdorff, E. 1996. Population responses of coastal zoobenthos to stress induced by drifting algal mats. Marine Ecology Progress Series **140**:141-151.
Norkko, J., Bonsdorff, E., and Norkko, A. 2000. Drifting algal mats as an alternative habitat for benthic invertebrates: species specific responses to a transient resource. Journal of Experimental Marine Biology and Ecology **248**:79-104.
O'Connor, N. E., Crowe, T. P., and McGrath, D. 2006. Effects of epibiotic algae on the survival, biomass and recruitment of mussels, *Mytilus* L. (Bivalvia: Mollusca). Journal of Experimental Marine Biology and Ecology **328**:265-276.
Ozimek, T., Pieczyńska, E., and Hankiewicz, A. 1991. Effects of filamentous algae on submerged macrophyte growth: A laboratory experiment. Aquatic Botany **41**:309-315.

Peterson, B. J., and Heck Jr, K. L. 2001. Positive interactions between suspension-feeding bivalves and seagrass-a facultative mutualism. Marine Ecology Progress Series **213**:143-155.
Peterson, C. H. 1982. Clam predation by whelks (*Busycon* spp.): experimental tests of the importance of prey size, prey density, and seagrass cover. Marine Biology **66**:159-170.
Peterson, C. H., and Beal, B. F. 1989. Bivalve growth and higher order interactions: importance of density, site, and time. Ecology **70**:1390-1404.
Posey, M. H., Wigand, C., and Stevenson, J. C. 1993. Effects of an introduced aquatic plant, *Hydrilla verticillata*, on benthic communities in the upper Chesapeake Bay. Estuarine, Coastal and Shelf Science **37**:539-555.
Rasmussen, J. R., Olesen, B., and Krause-Jensen, D. 2012. Effects of filamentous macroalgae mats on growth and survival of eelgrass, *Zostera marina*, seedlings. Aquatic Botany **99**:41-48.
Reusch, T., Chapman, A., and Groger, J. 1994. Blue mussels *Mytilus edulis* do not interfere with eelgrass *Zostera marina* but fertilize shoot growth through biodeposition. Marine Ecology Progress Series **108**:265-282.
Reusch, T. B., and Williams, S. L. 1998. Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia*. Oecologia **113**:428-441.
Reusch, T. B., and Williams, S. L. 1999. Macrophyte canopy structure and the success of an invasive marine bivalve. Oikos **84**:398-416.
Reusch, T. B. H. 1998. Differing effects of eelgrass zostera marina on recruitment and growth of associated blue mussels *Mytilus edulis*. Marine Ecology Progress Series **167**:149-153.
Semesi, I. S., Beer, S., and Björk, M. 2009. Seagrass photosynthesis controls rates of calcification and photosynthesis of calcareous macroalgae in a tropical seagrass meadow. Marine Ecology Progress Series **382**:41-47.
Sugimoto, K., Hiraoka, K., Ohta, S., Niimura, Y., Terawaki, T., and Okada, M. 2007. Effects of ulvoid (*Ulva* spp.) accumulation on the structure and function of eelgrass (*Zostera marina* L.) bed. Mar Pollut Bull **54**:1582-1585.
Tallis, H. M., Ruesink, J. L., Dumbauld, B., Hacker, S., and Wisehart, L. M. 2009. Oysters and aquaculture practices affect eelgrass density and productivity in a Pacific Northwest estuary. Journal of Shellfish Research **28**:251-261.
Taplin, K. A., Irlandi, E. A., and Raves, R. 2005. Interference between the macroalga *Caulerpa prolifera* and the seagrass *Halodule wrightii*. Aquatic Botany **83**:175-186.
Thiel, M., Stearns, L., and Watling, L. 1998. Effects of green algal mats on bivalves in a New England mud flat. Helgoländer Meeresuntersuchungen **52**:15-28.
Thiet, R. K., Smith, S. M., Rubino, V., Clark, R., Lee, K., and Oset, J. 2014. Soft shell clams (*Mya arenaria*) contribute to macroalgal blooms in a partially-restored Gulf of Maine back-barrier lagoon. Ecological Restoration **32**:46-58.
Thomsen, M., Stæhr, P., Nejrup, L., and Schiel, D. 2013. Effects of the invasive macroalgae *Gracilaria vermiculophylla* on two co-occurring foundation species and associated invertebrates. Aquatic Invasions **8**:133-145.
Tsai, C., Yang, S., Trimble, A. C., and Ruesink, J. L. 2010. Interactions between two introduced species: *Zostera japonica* (dwarf eelgrass) facilitates itself and reduces condition of *Ruditapes philippinarum* (Manila clam) on intertidal flats. Marine Biology **157**:1929-1936.
Tuya, F., Hernandez-Zerpa, H., Espino, F., and Haroun, R. 2013. Drastic decadal decline of the seagrass *Cymodocea nodosa* at Gran Canaria (eastern Atlantic): interactions with the green algae *Caulerpa prolifera*. Aquatic Botany **105**:1-6.
van der Heide, T., Govers, L. L., de Fouw, J., Olff, H., van der Geest, M., van Katwijk, M. M., Piersma, T., van de Koppel, J., Silliman, B. R., Smolders, A. J., and van Gills, J. A. 2012. A three-stage symbiosis forms the foundation of seagrass ecosystems. Science **336**:1432-1434.
Vinther, H. F., and Holmer, M. 2008. Experimental test of biodeposition and ammonium excretion from blue mussels (*Mytilus edulis*) on eelgrass (*Zostera marina*) performance. Journal of Experimental Marine Biology and Ecology **364**:72-79.

Wagner, E., Dumbauld, B. R., Hacker, S. D., Trimble, A. C., Wisehart, L. M., and Ruesink, J. L. 2012. Density-dependent effects of an introduced oyster, *Crassostrea gigas*, on a native intertidal seagrass, *Zostera marina.* Marine Ecology Progress Series **468**:149-160.

Wall, C. C., Peterson, B. J., and Gobler, C. J. 2008. Facilitation of seagrass *Zostera marina* productivity by suspension-feeding bivalves. Marine Ecology Progress Series **357**:165-174.

Ward, J. M., and Ricciardi, A. 2010. Community-level effects of co-occurring native and exotic ecosystem engineers. Freshwater Biology **55**:1803-1817.

Wright, J. T., Byers, J. E., Koukoumaftsis, L. P., Ralph, P. J., and Gribben, P. E. 2010. Native species behaviour mitigates the impact of habitat-forming invasive seaweed. Oecologia **163**:527-534.

Wright, J. T., and Gribben, P. E. 2008. Predicting the impact of an invasive seaweed on the fitness of native fauna. Journal of Applied Ecology **45**:1540-1549.

CHAPTER 3 DISTRIBUTIONS AND INTERACTIONS AMONG SEAGRASS AND SEAWEED AND ASSOCIATED SHELL-FORMING COMMUNITIES IN NEW ZEALAND ESTUARIES

Abstract

Foundation species are ecologically important organisms that buffer environmental stress, create habitat, and modify the surrounding environment. In marine systems, seagrass and seaweeds represent large and conspicuous habitat formers, whereas small, solitary, shell-forming bivalves and snails may provide less conspicuous but similar ecological functions. Many studies have documented distribution patterns of seagrass or seaweed in isolation, but few have quantified possible co-occurrence patterns or their combined effects on small solitary bivalves and snails. Here I address this research gap. First, I describe spatial distribution patterns of both the seagrass *Zostera muelleri* and seaweeds (mainly *Ulva* spp. and *Gracilaria chilensis*) via benthic 1m^2 photographs taken from 15 estuaries over three latitudinal regions in New Zealand, and their seasonal patterns from a single estuary over two years of sampling. Second, I test (also from survey data collected across latitudes and seasons), how the same seagrass and seaweeds affect abundances of shell-forming bivalves and snails. Finally, I tested in two field experiments, how these seagrass and seaweeds affect each other and shell-forming bivalves and snails. The latitudinal survey showed that seagrass and seaweeds were present in all 15 estuaries, co-occurring in 25% (343) of the samples, while 13% contained no seagrass or seaweed. In addition, seagrass and seaweeds co-occurred in 62% (618) of the samples from the local seasonal survey, while 6% had neither seagrass nor seaweed. Across all the sampled estuaries bivalves and snails were, compared to bare mudflats, 32% and 73% more abundant in the presence of seagrass and seaweed, respectively, with relatively little additional positive effects when they co-occurred. These results were at least partially supported experimentally. Snails and bivalves were 400-500% more abundant in the presence of seaweed (depending on experimental conditions and seaweed biomass), but with relatively little additional positive effect by seagrass. Most of this strong facilitative effect occurred because many small snails inhabited the seaweed mats. Seagrass root biomass was reduced by 35 and 81% in the presence of the highest *Ulva* addition levels in the two experiments whereas leaf biomass in the undisturbed seagrass control plot was almost 80% lower in the high *Ulva* treatment (second experiment only). In conclusion, seagrass and seaweeds are common, and often co-occurring, foundation species in New Zealand estuaries, with strong positive effects on shell-forming snails and bivalves.

However, seaweed have, when occurring in high abundances, negative effect on seagrasses themselves. Future studies should aim to identify thresholds and environmental conditions where effects of seaweed on seagrass changes from neutral to negative, as well as examine how facilitated shell-forming bivalves and snails may further modify community structures and ecosystem functions.

Introduction

Ecosystems are often dominated by a few habitat-forming organisms, often referred to as foundation species (Dayton 1972, Ellison et al. 2005). These organisms, including trees, corals, mangroves, kelp, and seagrass, lay the functional framework (the foundation) for communities by creating habitat, mediating community interactions, controlling populations, and regulating ecosystem dynamics (Dayton 1972, Ellison et al. 2005). For example, in forests, trees create physical habitat and alter microclimates (Coates et al. 1991, Ellison et al. 2005), on rocky shores, canopy-forming seaweed reduce stress for other organisms and buffer them from wave action (Molina-Montenegro et al. 2005, Schiel and Lilley 2007), and desert trees can act as nurse plants for cacti and other shrubs (Valiente-Banuet and Ezcurra 1991, Bashan et al. 2009).

Foundation species and their associated communities vary spatially in abundances and relative importance, from fine-scale neighbourhoods to broad-scale geographic ranges, depending on environmental, physical, and trophic conditions (Chesson 1985, Shank et al. 1998, Airoldi 2000, Schiel and Lilley 2011, Angelini et al. 2015, Donadi et al. 2015). For example, different canopy-forming seaweed species have different tolerances for wave energy, light levels, and desiccation stress, causing zonation patterns on rocky shores (Connell 1961, Lubchenco 1980, McQuaid 1982, Schiel 2011). Likewise, subalpine trees occupy different elevation bands on mountains because of environmental or resource limitations (Rochefort et al. 1994, Macias-Fauria and Johnson 2013). Trophic interactions can also control foundation species, such as urchins that regulate abundances of kelp, or deer altering forest structure through browsing (Paine and Vadas 1969, Chapman 1981, Rooney 2001). Foundation species also vary in time, as biogeographical patterns and distributions of ecosystems observed in the present, were formed through past processes such as glaciation and evolutionary events (Morris 1990). These processes still shape foundation species and associated communities today, along with smaller-scale processes, such as disturbance events or seasonal variation. Similarly, foundation species change through time following

disturbances and succession events, such as seaweed community composition on a rocky shore after a long-term press disturbance (Schiel 2011, Schiel and Lilley 2011), or changes to dominant trees in a forest following a logging event (Abrams and Scott 1989).

A 'foundation species' is typically not a single species but instead represented by groups of co-occurring and functionally similar species, like tree species in a forest or canopy-forming seaweed species on a rocky shore. These co-occurring foundation species may thereby compete with or facilitate each other (see also Chapter 1 and 2). In estuaries, there are three general types of foundation species; rooted perennial and clonal seagrasses (den Hartog 1970, Brasier 1975, Green and Short 2003), drift and attached ephemeral seaweed (macroalgae) (Lavery et al. 1991, Hernández et al. 1997, Gribben and Wright 2006), and shell-forming organisms such as bivalves, snails, and some polychaetes (Dauer et al. 1982, Abbe 1988, Callaway et al. 2010, Wernberg et al. 2010, Thomsen et al. 2016) as well as their dead calcareous shells and tubes (Kidwell and Jablonski 1983, Ayres-Peres and Mantelatto 2010). These estuarine foundation species all provide complex, three-dimensional habitat potentially facilitating surrounding communities, resulting in patchy areas of high biodiversity (Bell et al. 2001, Boström et al. 2006, Thomsen 2010, Wright et al. 2014, Thomsen et al. 2016, Hanke et al. 2017). Seagrasses, seaweeds, and shell-formers have typically been studied in isolation (Turner et al. 1999, Jones and Pinn 2006, Sousa et al. 2009) or, less commonly, in pairs (e.g., documenting effects of seaweed on seagrass, see Chapter 2) (Irlandi 1997, Huntington and Boyer 2008, Yarrington et al. 2013). In contrast, few studies have documented distributions and effects of seagrass, seaweeds, and shell-formers on each other even though these types of foundation species have been reported to co-occur (Micheli and Peterson 1999, Jupp et al. 2007, Cacabelos et al. 2012).

The main objective of this chapter is to quantify distribution patterns and interactions between the seagrass *Zostera muelleri*, seaweeds (mainly *Ulva spp*. and *Gracilaria chilensis*), and shell-formers (bivalves such as *Mytilus edulis* and snails like *Micrelenchus huttonii*). These organisms were chosen to study as they are relatively common in New Zealand estuaries (Logan 1976, Jones et al. 2005, Battley et al. 2011, Thomsen et al. 2016, Carson and Morris 2017) - but little is known about where they co-occur and how they affect each other. Specifically, I hypothesize that:

1) Seagrass and seaweeds are common and co-occur across latitudes, estuaries, sites and seasons on the South Island of New Zealand.

2) Seagrass and seaweeds have positive effects on shell-forming snails and bivalves compared to unvegetated sediments because they form and modify biogenic habitats (Boström et al. 2006, Thomsen et al. 2013).
3) Seaweed have negative effects on seagrass due to shading and smothering (Short and Wyllie-Echeverria 1996, Cummins et al. 2004), mussels have positive effects on seagrass and seaweed through nutrient deposition (Wall et al. 2008, Wagner et al. 2012) and seagrass have positive effects on seaweed by increasing retention (Wernberg et al. 2006, Biber 2007).

Methods

Study Areas

To examine large scale distribution patterns of seagrass and seaweeds, 15 estuaries were sampled in 2016 on the South Island of New Zealand (Figure 3.1). In April 2016 six northern estuaries were sampled: Ruataniwha Inlet (40°39'10.2"S 172°40'35.5"E), Puponga Coast (40°31'36.1"S 172°44'03.6"E), Nelson Haven (41°13'51.4"S 173°18'33.4"E), Delaware Bay (41°10'05.6"S 173°26'33.6"E), Okiwa Bay (41°15'54.8"S 173°54'57.2"E) and Ngakuta Bay (41°16'22.6"S 173°57'48.4"E). Three estuaries were sampled centrally in February 2016: Avon-Heathcote Estuary (43°32'58.1"S 172°44'33.6"E), Duvauchelle Bay (43°45'11.4"S 172°55'44.6"E), and Robinsons Bay (43°45'51.9"S 172°57'28.6"E). Finally, six southern estuaries were sampled in October 2016: Portobello Bay (45°49'21.6"S 170°39'58.3"E), Papanui Inlet (45°50'32.7"S 170°41'33.0"E), Dowling Bay (45°47'18.9"S 170°39'46.8"E), Catlins River Estuary (46°28'47.3"S 169°41'17.3"E), Jacob's River Estuary (46°20'52.7"S 168°00'56.3"E), and New River Estuary (46°25'47.6"S 168°20'18.3"E). These chosen estuaries have extensive seagrass beds and seaweeds are common, are tidal and shallow with sandy to muddy sediments, and have gentle slopes. Additional surveys were carried out in the Avon-Heathcote Estuary (Figure 3.1) to examine small-scale spatio-temporal variation of seagrasses and seaweeds over two years. The Avon-Heathcote Estuary is surrounded by the city of Christchurch, New Zealand, and is a ca. 8.8 km^2 shallow, well-flushed, bar-built estuary. Two rivers flow into the estuary; the Avon River flows from the north and the Heathcote from the southwest (Figure 3.1). Seagrass beds are abundant along the eastern side of the estuary where they cover ca. 0.35 km^2 (Hollever and Bolton-Ritchie 2016).

Distribution of seagrasses and seaweeds

Latitudinal survey

To investigate if seagrass and seaweeds co-occur across latitudes and estuaries on the South Island of New Zealand (Figure 3.1) digital photos were taken 90 cm from, and perpendicular to, the substratum with a Nikon AW 130 camera. Transects were chosen in proximity to known seagrass beds. This method has previously been ground-truthed to unit area (1 m^2) by taken photos of transect tapes (Thomsen et al. 2018a). Photos were taken ca. every 2 m during low tide, by walking a straight transect line from the shore to the water's edge, thereby sampling all benthic habitats encountered on the transect. A range of 76-872 photos were taken from each of the 15 sampled estuaries (average 268 ± 46 photos · $estuary^{-1}$), depending on the size of the sampled area and water level at the time of sampling. A random subset of the photographs (n = 90 per estuary, except New River, n = 76) were analysed visually for percent cover of seagrass, seaweeds, surface-dwelling dead shells, unvegetated sediments, and rock. This is a fast method to collect spatially extensive data, but it only provides a conservative estimate of abundances because it cannot detect foundation species hidden underneath other species. It was typically not a problem to identify co-occurring seagrass and seaweed from image analysis, but shell-forming snails and bivalves often hide in the vegetation, so a specific survey was done to quantify their abundances in different habitats (see below).

First, a Spearman rank correlation analysis was used to test for possible positive or negative relationships between cover of seagrass and seaweed. Second, analysis of variance (ANOVA) were used to test if seagrass or seaweed cover varied between regions and estuaries (cover was normalised by arcsine square-root transformation, see Chapter 5 for the statistical analysis of dead shells). Homogeneity of variances was checked with Levene's test (package *'car'*). Test were evaluated with alpha = 0.05, unless variances could not be transformed to homogeneity, where after alpha was reduced to 0.01. If ANOVA tests were significant, treatment effect were determined with Tukey's Honest Significant Difference post hoc tests. All analyses were done in R version 3.5.0 (R Core Team 2017).

Temporal survey

To examine if seagrass and seaweeds co-occur across sites, seasons and years, digital photos were taken from two sites (near Plover and Tern Streets, Figure 3.1) in the Avon Heathcote estuary in winter and summer months (twice a season, both early and late) from 2014-2016,

using the same methods as described for the latitudinal survey. The exact same transects were not used at each sampling time but were similar in location and habitats. Generally, 90 images were collected per site and sampling event, except for (a) May 2015 where n = 40 and 47 for Plover and Tern, (b) March 2016 where n = 49 for Plover, and (c) November 2015 where n = 49 for Tern. Percent cover of seagrass and seaweed were analysed for correlations and effects of season and sites as described for the latitudinal survey.

Effects of seagrass and seaweed on shell-forming invertebrates

Latitudinal survey

To examine if seagrass and seaweed influenced shell-forming invertebrate communities across latitudes, three circular cores (9 cm diameter × 10 cm depth) were collected from the 15 estuaries described above (Figure 3.1) from four habitats: bare sediments, sediments covered by seaweeds (mainly *Ulva* or *Gracilaria chilensis*), sediments covered by seagrass (*Zostera muelleri*), and sediments covered by co-occurring seagrass and seaweed. Sampled cores were placed into labelled 1 mm mesh bags, rinsed in the field to remove sediments, and placed in a -20 ˚C freezer within 4 hours of sampling. If an estuary contained more than one seaweed species, cores were collected for each of them. Cores were collected from both the mid intertidal and the upper subtidal zones. The minimal sampled number of cores per estuary was 24 (4 habitat types × 2 elevation levels × 3 replicates). In the lab, shell-forming organisms were identified and counted. Shell-forming taxa included *Austrovenus stutchburyi*, *Macomona liliana*, *Paphies australis*, *Linucula hartvigiana*, *Venerupis* sp., *Tawera spissa*, *Mytilus edulis*, and *Panopea zelandica* (bivalves) and *Notoacmea* spp., *Diloma nigerrimum*, *Micrelenchus huttonii*, *Amphibola crenata*, *Cominella glandiformis*, *Zeacumantus subcarinatus*, *Buccinulum linea*, and *Lunella smaragda* (gastropods). Seaweed and seagrass (separated into aboveground leaves and belowground root and rhizomes) were dried at 55° C for 72 hours and weighed. ANOVAs were used to test if densities (converted to m^{-2}) and taxonomic richness of shell-formers were affected by latitudinal region, estuary, tidal elevation, and habitat. Assumption tests and post-hoc tests were as described in the photo-surveys. If variance homogeneity assumptions were violated, data were transformed (log 10 or square root) and if variances were still heterogeneous, alpha was reduced to 0.01.

Temporal survey

Additional cores were collected to study if seagrass and seaweeds influence shell-former densities and taxonomic richness across sites (Plover vs. Tern Streets), seasons (winter vs. summer) and years (2014-2016, see 'Distributions: Temporal survey' for more details). Cores were collected with the same methodology as described for the latitudinal survey from the same four habitats (bare sediment, *Zostera*, *Ulva*, and *Zostera+Ulva*). At each sampling events four cores were taken from each habitat. Samples were processed as described in the latitudinal survey. Shell-forming taxa found in this survey included the bivalves *Austrovenus*, *Macomona*, and *Mytilus*, and the gastropods *Notoacmea*, *Diloma*, *Micrelenchus*, *Amphibola*, *Cominella*, and *Buccinulum*. ANOVAs were used to test if densities and richness of shell formers varied between year, season, tidal elevation, site, and habitats. Assumption tests and post-hoc tests were similar done as described for the latitudinal survey.

Field Experiment 1: effects of seagrass, seaweed and mussels

A 3 × 3 factorial experiment tested for density-dependent effects of seagrass, seaweed and mussels on other shell-forming invertebrates. Mussels were used in this experiment as they commonly co-occur with seagrass beds worldwide (Valentine and Heck 1993, Grizzle et al. 1996, Reusch 1998, Bologna and Heck 2000, Hendriks et al. 2011, Thomsen et al. 2013). Circular plots (108, 40 cm diameter, separated by 1m) were established in a seagrass bed in the Avon-Heathcote Estuary on 17 April 2015. Each plot was marked with a centre-stake and allocated to one of 27 treatment-combinations (*Ulva*, mussels, seagrass × each with 3 nested abundance treatments, $n = 4$, more details below). Abundances of seagrass were manipulated by cutting all leaves at the sediment surface (with a pair of scissors ~40 cm diameter, 0% remaining = 'removed)', by cutting leaves to half their length (50% remaining = 'cut'), and by leaving leaves intact (100% remaining = 'control'). Abundances of mussels were manipulated by adding 0, 1, or 4 *Mytilus* to the center of each plot, which is higher than average for most areas within the Avon-Heathcote Estuary. Finally, abundances of *Ulva* were manipulated by adding 0, 150 or 500 mL wet seaweed volume to the center of the plot, which were similar to amounts found in the estuary during a non-bloom period. The seagrass treatment was applied first, followed by mussel (pushed slightly into the sediment, umbo first, around the central stake for byssal attachment) and then seaweed additions (staked down with five u-bend metal pegs). All plots were disturbed in the same manner to avoid experimental artefacts, that is, seagrass and mussel controls were disturbed with hands to

simulate removals and additions, and five metal pegs were added to control plots (see Supplementary Material for example treatments). Treatments were re-applied, if necessary, every 7-10 days (if organisms had died or washed away). The experiment was terminated on 4 June 2015 where a centre core was collected (see surveys). Field sampling and laboratory processing was as described for the surveys. ANOVAs were used to test for effects of species identity and abundance of the three foundation species on densities and richness of shell-forming organisms. In addition, effects of mussel and seaweed additions were tested on seagrass root biomass, and effects of seagrass and mussel treatments on seaweed biomass. The treatment of seaweed effects on seagrass leaves was not analysed due to interfering factors (see Field Experiment 2). Assumption tests and post-hoc tests were conducted as described in the previous surveys.

Field Experiment 2: effects of seagrass and seaweed

In experiment 1, it is possible that a small amount of drifting seagrass debris became entangled to the added seaweed mats during the experiment, potentially interfering with the analysis of how seaweeds affected the seagrass leaves. In addition, experiment 1 could not distinguish between if shell forming snails and bivalves were more common associated with added *Ulva* mats or with the seagrass/sediment habitat. Experiment 1 was therefore repeated (but without mussel treatments because mussels had few effects) taking great care that added seaweed did not contain any seagrass debris (or snails/bivalves). The experimental design and methods were otherwise as described for experiment 1, with three replicates for each of the 9 treatment combinations. Experiment 2 was initiated on 27 November 2015, maintained every 7-10 days and terminated on 28 January 2016. At the end of the experiment, all seaweed was first collected from each plot centre into separate plastic bags, where afterwards cores were collected as described for experiment 1. The cores and corresponding *Ulva* bags were placed into labelled 1 mm mesh bags and washed in the field to remove sediments and placed into a -20°C freezer within 2 hours of sampling. Cores and *Ulva* bags were processed as described for experiment 1. ANOVA was again used to test for effects of seaweed and seagrass on densities and richness of shell-forming organisms. A pairwise t-test was conducted to examine if there were differences in densities and taxonomic richness of shell-forming bivalves and snails between pairwise samples epibenthic *Ulva* mats vs. sediment cores (with seagrass leaves and roots). Effects of seaweed additions were also tested on seagrass root biomass, and effects of seagrass on seaweed biomass with ANOVAs. Assumption tests and

post-hoc tests were as described in the surveys. Finally, I tested if seaweed trapped drifting seagrass by correlating the biomass of the seaweed *Ulva* with the seagrass biomass found within the seaweed mats (with Spearman's rank coefficient because data were not normally distributed).

Results

Distribution of seagrass and seaweed

Latitudinal survey

In the latitudinal survey, 25% (343) of all images contained both seagrass and seaweed, 37% only seagrass, 23% only seaweed, and 13% had neither of them. There was a significant negative relationship between seagrass and seaweed cover (rho = -0.27, p <0.001, Figure 3.2). Seagrass cover differed between latitudinal regions ($p < 0.001$) and estuaries ($p < 0.001$, Table 3.1A). The central region had the highest average seagrass cover (24.6 ± 1.4% image^{-1}), followed by the southern region (21.2 ± 1.1%), and then the northern region (20.9 ± 1.0%). More specifically, Papanui Inlet had the highest cover (39.8 ± 3.1%), followed by Duvauchelle Bay (32.2 ± 3.2%), while Ruataniwha Inlet and New River Estuary had the least (11.0 ± 1.8% and 5.9 ± 1.6% respectively, Figure 3.3).

Seaweed cover also varied between regions ($p < 0.001$) as well as estuaries ($p < 0.001$, Table 3.1B). The southern region hosted the highest seaweed coverage (12.4 ± 1.0% image^{-1}), followed by the northern (4.7 ± 0.4%) and central regions (4.5 ± 0.6%). Dowling Bay had the most seaweed cover (42.4 ± 3.4%), followed by Jacobs River Estuary (11.6 ± 1.9% photo^{-1}), while the estuaries with the least coverage were the Avon-Heathcote Estuary (1.4 ± 0.4%) and Portobello Bay (1.1 ± 0.4%, Figure 3.3).

Temporal survey

Co-occurring seagrass and seaweed were found in 62% (618) of the analysed images, while 12% only had seagrass, 19% only had seaweed, and 6% had neither seagrass nor seaweed. There was a significant positive relationship between seagrass and seaweed percent cover (rho = 0.11, $p < 0.001$, Figure 3.4). Seagrass cover varied between sample years ($p < 0.001$), but not seasons ($p = 0.934$) or sample site ($p = 0.013$, Table 3.2A). The second sample year (2016) had higher seagrass cover (25.2 ± 0.7% image^{-1}) than the 2015 sample year (18.7 ± 1.0%, Figure 3.5). Seaweed cover varied between both years and season ($p < 0.001$, Table

3.2B), with higher cover in the 2015 sample year (12.2 ± 0.7%), than in 2016 (6.9 ± 0.4%), but higher coverage in the summer (13.0 ± 0.6%), than winter (4.7 ± 0.3%). Seaweed cover also differed between sample sites ($p < 0.001$, Table 2B), with Plover Street showing higher coverage (11.3 ± 0.7%) than Tern Street (7.7 ± 0.4%, Figure 3.5).

Effects of seagrass and seaweed on shell-forming organisms

Latitudinal survey

Shell-forming taxa generally dominated the community composition in the processed samples, varying from ca. 40-90% of the counted organisms per estuary (Figure 3.6A). Densities of shell-formers (log 10 +1 transformed) had several significant interactions between estuaries, tidal elevations, and the presence of seagrass and seaweed ($p < 0.001$, Table 3.3A), as well as latitudinal region (Region × Seagrass, $p = 0.001$, Region, $p < 0.001$). However, there was no significant interaction between seagrass and seaweeds ($p = 0.290$). The factor 'estuary' accounted for most of the high data variability in this test (highest sum of squares, Table 3.3A). The Avon-Heathcote Estuary had the highest densities of shell-forming organisms (4813.7 ± 1172.6 m^{-2}) followed by Puponga Bay (2125.7 ± 264.0 m^{-2}), while lowest densities were found in Dowling Bay (239.5 ± 52.7 m^{-2}) and New River Estuary (62.9 ± 28.7 m^{-2}, Figure 3.6B). Shell-formers were more abundant in seagrass beds (1542.1 ± 113.1 m^{-2}) and seaweed weed (1664.2 ± 134.5 m^{-2}) than on mudflats (957.1 ± 72.2 m^{-2}). Across latitudes, shell-formers were most abundant in the central region (2235.9 ± 467.7 m^{-2}), with intermediate abundances in the northern region (1529.3 ± 80.9 m^{-2}), and lowest abundances in the southern region (890.4 ± 93.5 m^{-2}) (Figure 3.6B).

Species richness of shell-formers varied between estuary and tidal elevation ($p = 0.004$, Table 3.3B). Across estuaries, highest taxonomic richness was found in Ngakuta Bay (4.3 ± 0.3 $core^{-1}$) and Okiwa Bay (3.9 ± 0.2 $core^{-1}$), and with lowest richness in Dowling Bay (0.9 ± 0.2 $core^{-1}$) and New River Estuary (0.3 ± 0.1 $core^{-1}$). Richness of shell-formers was also affected by latitudinal region ($p < 0.001$), with highest richness found in the northern region (3.6 ± 0.1 $core^{-1}$), intermediate richness in the central region (2.5 ± 0.2 $core^{-1}$), and lowest richness in the southern region (1.8 ± 0.1 $core^{-1}$). Finally, richness was higher in seagrass beds (2.8 ± 0.1 $core^{-1}$) and seaweed beds (3.0 ± 0.1 $core^{-1}$) compared to mudflats (2.3 ± 0.1 $core^{-1}$, Table 3.3B, Figure 3.6C).

Temporal survey

Densities of shell-forming taxa (log 10+1 transformed) were affected by several interactions, including the test factors year, season, tidal elevation, and presence of seaweed and seagrass (Table 3.4A), where seagrass and seaweed test factors explained most of the sum of square data variability (Table 3.4A). Pooled across test-factors (Figure 3.7A-D), densities were higher in 2015 (4694.6 ± 439.7 m^{-2}) than 2016 (3323.5 ± 308.5 m^{-2}), in winter (5448.2 ± 464.5 m^{-2}) than summer (2574.8 ± 220.1 m^{-2}), and in the subtidal (4657.7 ± 426.9 m^{-2}) than intertidal (3391.7 ± 333.8 m^{-2}) (there was no effect of sites). More specifically, a strong significant interaction between seagrass and seaweeds ($p < 0.001$) revealed that co-occurring seagrass and seaweed had highest densities (7439.2 ± 640.0 m^{-2}), followed by seaweed along (5016.9 ± 574.5 m^{-2}), seagrass alone (2920.2 ± 257.5 m^{-2}), and bare sediment (739.3 ± 93.3 m^{-2}, Figure 3.7E).

Richness of shell-formers was also affected by many interactions including various combinations of year, season, site, seagrass and seaweed (Table 3.4B), of which year explained most of the sum of square data variability (Table 3.4B). Pooled across test-factors (Figure 3.8A-D) richness was higher in 2015 (3.6 ± 0.2 $core^{-1}$) than 2016 (2.5 ± 0.1 $core^{-1}$), in summer (3.2 ± 0.2 $core^{-1}$) than winter (2.8 ± 0.1 $core^{-1}$), and at Tern Street (3.4 ± 0.2 $core^{-1}$) than Plover Street (2.7 ± 0.1 $core^{-1}$). Results from the significant seagrass × seaweed interaction ($p = 0.039$) showed again higher richness in presence of co-occurring seaweed and seagrass (3.4 ± 0.2 $core^{-1}$), followed by seaweed alone (3.3 ± 0.2 $core^{-1}$), seagrass alone (3.1 ± 0.2 $core^{-1}$), and bare sediments (2.3 ± 0.2 $core^{-1}$, Figure 3.8E).

Field Experiment 1: effects of seagrass, seaweed and mussels

Densities of shell-formers were affected by the presence of *Ulva* ($p < 0.001$) but not seagrass ($p = 0.844$) or mussels ($p = 0.681$, Table 3.5A, Figure 3.9A, C, E; there were no significant interactions). More specifically, densities were highest at high *Ulva* levels (500 mL; 20385.8 ± 1804.5 m^{-2}), intermediate at mid-levels (150 mL, 18591.3 ± 1534.2 m^{-2}), and lowest in the controls (3868.5 ± 1009.3 m^{-2}, Figure 3.9). Richness was affected by the *Ulva* × mussel interaction ($p = 0.009$) and mussels alone ($p = 0.037$) but not seagrass ($p = 0.726$, Table 3.5B, Figure 3.9B, D, F). However, follow up post hoc tests only found significant differences between 4mussels+0*Ulva* vs. 0mussels+0*Ulva* ($p = 0.002$) and 4mussel+500*Ulva* vs 4mussel+0*Ulva* ($p = 0.017$). Pooled across other test factors, richness was highest in treatments with 4 mussels (3.9 ± 0.2 $core^{-1}$), intermediate with 1 mussel (3.6 ± 0.2 $core^{-1}$), and

lowest without mussels (3.3 ± 0.1 core^{-1}, Figure 3.9). Seagrass root biomass was affected by the seagrass × mussel interaction (p = 0.017) and *Ulva* additions (p = 0.046, Table 3.6A) but with no clear patterns between treatment-combinations, except that biomass generally was highest in the undisturbed seagrass controls (Figure 3.10A). For the seaweed treatments, root biomass was highest in control plots (0.42 ± 0.04 g·core^{-1}) and lowest under high (500 mL) seaweed levels (0.31 ± 0.03 g·core^{-1}, Figure 3.10B). Finally, there were no effects of either seagrass (p = 0.593), mussels (p = 0.772), or their interaction (p = 0.978) on seaweed biomass (Table 3.6B).

Field Experiment 2: effects of seagrass and seaweed

Overall, densities of shell-formers were not affected by experimental seagrass treatments (p = 0.535), seaweed additions (p = 0.041) or their interaction (p = 0.518, Table 3.7A, Figure 3.11A, C). Taxonomic richness of shell-formers was significantly affected by seagrass treatment (p = 0.009), but not seaweed addition (p = 0.247) or the seagrass × seaweed interaction (p = 0.498, Table 3.7B, Figure 3.11B, D). Species richness was highest at the intermediate 'cut' seagrass levels (3.0 ± 0.3 core^{-1}), followed by undisturbed controls (2.4 ± 0.2 core^{-1}), and lowest in the full seagrass removals (2.0 ± 0.2 core^{-1}, Figure 3.11B). There was no difference in taxonomic richness between the entangled seaweed mats and the seagrass/sediment cores (t = -1.638, p – 0.119).

Seagrass leaf biomass was highest in plots without *Ulva* (0.86 ± 0.15 g) and lowest in plots with highest *Ulva*-levels (0.18 ± 0.06 g, Figure 3.12A; only tested in the un-manipulated seagrass control plots, p = 0.014, Table 3.8A). Seagrass root biomass was also affected by seaweed addition (p = 0.009), but not seagrass treatments (p = 0.951) or the seaweed × seagrass interaction (p = 0.263, Table 3.8B). Seagrass root biomass was, like for seagrass leaves, highest in plots without *Ulva* (0.69 ± 0.08 g) and lowest in plots with highest *Ulva* (0.38 ± 0.05 g, Figure 3.12B). Drifting seagrass material was found entangled within the *Ulva* mats in both the low and high *Ulva* addition plots (0.023 ± 0.005 vs. 0.033 ± 0.010 g seagrass material), but there was no relationship between seaweed and entrained seagrass biomass (Spearman's rank, p = 0.212). Finally, I found no effects of seagrass cover on the retention of seaweed biomass (p = 0.434, Table 3.8C).

Discussion

Foundation species are ecologically important organisms that provide physical habitat, ecosystem functioning and ecosystem services (Dayton 1972, Ellison et al. 2005). Here I showed that seagrass, seaweed and shell-forming bivalves can all be considered foundation species that often co-occur in estuaries across the South Island of New Zealand, as they interact and influence the benthic communities around them.

Distributions of estuarine foundation species

As hypothesized, seagrass and seaweeds were found, often co-occurring, at all sampled latitudes, estuaries, seasons, and sites on the South Island of New Zealand. Specifically, seagrass and seaweeds co-occurred in 25% of the samples from 15 estuaries, and >60% of the samples from the Avon-Heathcote temporal survey. The difference in co-occurrences between the two surveys likely arise from natural variation in seagrass and seaweed population sizes between estuaries in New Zealand. *Zostera muelleri*, a perennial seagrass, is relatively common in estuaries (Inglis 2003) but varies in biomass, leaf density, and patch size within and between estuaries (Turner et al. 1999, Inglis 2003, Turner and Schwarz 2006, Mills and Berkenbusch 2009, Battley et al. 2011). Estuarine seaweeds, such as *Ulva* spp. and *Gracilaria chilensis*, are also common in New Zealand estuaries (Henriques 1980, Pickering et al. 1990, Schiel and Nelson 1990, Heesch et al. 2009, Fry et al. 2011, Hollever and Bolton-Ritchie 2016). However, abundances of seaweed typically fluctuate more than seagrass across seasons, years, and sample sites, due to differences in in nutrient conditions, urbanization, temperature, substrate conditions, and hydrodynamic flow rates (Raffaelli et al. 1998, Thomsen and McGlathery 2007, Thomsen et al. 2007b, Marsden and Knox 2008, Abreu et al. 2011, Zhang et al. 2016). Most of the above listed studies have examined distributions of seagrass or seaweeds in isolation, or, more rarely, together in a single sample location, but I showed that seaweeds and seagrasses often co-occur across scales across the South Island of New Zealand.

Effects of seagrass and seaweed on shell-forming bivalves and snails

The presence of both seagrass and seaweeds had generally, as hypothesized, positive effects on both densities and richness of shell forming snails and bivalves. While both seagrass and seaweeds have been shown to be important habitat formers in marine systems, by creating hotspots of biodiversity (Boström et al. 2006, Thomsen 2010, Cacabelos et al. 2012, Wright

et al. 2014), they may have different functions. For example, seagrasses are perennial clonal organisms that often facilitate other organisms year-round in relatively large and stable beds (Duarte et al. 2006, Turner and Schwarz 2006, Short et al. 2007, van der Heide et al. 2007). Seagrass stabilize sediments with their roots and rhizomes (Reise 2002, Newell and Koch 2004), provide complex above-ground habitat (Heck and Orth 1980, Bell et al. 2001, Boström et al. 2006), buffer hydrodynamic forces (Fonseca et al. 1982, Fonseca and Cahalan 1992) and facilitate recruitment of bivalves and snails (Bologna and Heck 2000, Boström and Bonsdorff 2000, Connolly and Hindell 2006). Most estuary seaweeds, including *Ulva* spp. and *Gracilaria chilensis*, are ephemeral, providing a more fluctuating above-ground habitat (Norkko et al. 2000, Thomsen 2010, Wright et al. 2014, Thomsen et al. 2016). In contrast to seagrass, many macroalgae can also be a direct food source for grazers such as snails and limpets (Geertz-Hansen et al. 1993, Hauxwell et al. 1998, Berezina et al. 2005, see also Chapter 6). Furthermore, also unlike seagrasses, ephemeral seaweeds can bloom temporarily and form dense mats, which may have negative effects on some shell-forming organism, such as infaunal bivalves (Everett 1991, Valiela et al. 1997, Raffaelli et al. 1998, Lyons et al. 2014), thereby switching from a facilitative to a negative effect.

While I found no additional effects on shell-forming taxa when seagrass and seaweeds co-occurred in the latitudinal survey, there was a synergistic positive effect in the temporal survey in the Avon-Heathcote Estuary. This difference is likely caused by unusually high densities of the snail *Micrelenchus huttonii* in the Avon-Heathcote Estuary. *Micrelenchus* is facilitated by three-dimensional biogenic habitats, including seagrasses and seaweeds (Grange 1979, Henriques 1980, Taylor 1997, Marshall 1998, Thomsen et al. 2016, see also Chapter 6), where the seaweeds also provide a direct food-source (Chapter 6). Experimental data from the Avon-Heathcote Estuary, support that trochid snails (*Micrelenchus huttonii* and *Diloma subrostrata*) are facilitated by *Ulva* spp. and seagrass compared to bare sediments (Thomsen et al. 2016). Other studies have also found a positive effect of seagrasses and seaweeds on shell-forming organism abundances. For example, Cummins et al. (2004) found up to 4 times more mud snails (*Potamopyrgus antipodum*) when seaweed was added to experimental seagrass plots, and Holmquist (1997) detected six times more invertebrates in the presence of biogenic habitat, and up to thirty times more gastropods, compared to un-vegetated mud-flats. Unattached seaweed entangled around seagrass leaves, can also be an important food source for grazers (Zimmerman et al. 1979, Wernberg et al. 2006, Chapter 6) and may increase habitat complexity and offer shelter for mobile organisms (Heck and Orth

1980, Norkko et al. 2000, Thomsen 2010, Thomsen et al. 2013). In concert, mechanisms associated with provisioning of attachment space, food, and shelter from abiotic stress and predators, likely explain why shell-formers were found in high densities associated with seaweed, both on mudflats and within seagrass beds.

Effects of mussels and seaweed on seagrass

Mussels had complex effects on below ground seagrass biomass, so the hypothesis that mussels facilitate seagrass was only partially supported. Below ground biomass was generally higher in undisturbed seagrass plots in the presence of mussels, possibly because mussels can increase nutrient levels, stabilize sediments, and clarify the water column during high tide (Peterson and Heck Jr 2001b, Booth and Heck Jr. 2009, Thomsen et al. 2013, Sanmartí et al. 2018). However, there was no facilitation of below-ground biomass in the seagrass 'removal' and 'cut' treatments, suggesting that roots and rhizomes may have been under stress (Halun et al. 2002, Biber et al. 2009, Holmer et al. 2011). Seagrass below-ground biomass was, as hypothesized, negatively affected by the seaweed *Ulva*. Negative effects of seaweed have been shown before and can be attributed to low pore-water oxygen levels and toxic levels of sulphide and ammonia (Short and Wyllie-Echeverria 1996, Hauxwell et al. 2001, McGlathery 2001, Holmer and Nielsen 2007). *Ulva* also, as hypothesized, had negative effects on seagrass leaf biomass. Overall, negative effects of drift seaweeds on seagrass can arise from a combination of competition for light and nutrients (Coffaro and Bocci 1997, Brun et al. 2003a, Brun et al. 2003b, Mvungi et al. 2012), smothering during blooms, and development of anoxia, sulphides and ammonia in the sediment pore water (den Hartog 1994, Holmer et al. 2011, Höffle et al. 2012, Mvungi et al. 2012, Han and Liu 2014). I also documented, in my experiment, that *Ulva* can 'capture' and entrain drifting seagrass leaves, roots, and rhizomes. This entrainment into seaweed patches, could potentially facilitate dispersal of establishment of new seagrass patches (Hall et al. 2006). Seaweeds have been shown to be a dispersal agent for invertebrates, fish, and other seaweed (Kulczycki et al. 1981, Helmuth et al. 1994, Holmquist 1994, Ingólfsson 1995, Gagnon et al. 2015). However, no studies have shown that seaweeds can retain seagrass, and seagrass studies rarely address drifts of seagrass at all (see Wolff 1976, Josselyn et al. 1983, Kilar and Norris 1988, Harwell and Orth 2002, Hall et al. 2006, Heck et al. 2008, Vanderklift and Wernberg 2008, Britton-Simmons et al. 2012). To my knowledge this is the first documentation that seaweed can also entrain drifting seagrass leaves and roots.

Effects of seagrass and mussels on seaweed

There were no experimental effects of seagrass on seaweed biomass, so my hypothesis that seagrass would entrain seaweed was rejected. However, several other studies have shown that seagrass can entrain, and aid dispersal, of seaweed (Virnstein and Carbonara 1985, Bell et al. 1995, Bell and Hall 1997, Kopecky and Dunton 2006, Sfriso et al. 2012). My no-effect results may be explained by differences in seagrass properties (e.g., density, length of leaves), current velocities, freshwater runoff (including fertilizers and pesticides), and grazer abundances (Virnstein and Carbonara 1985, Bell and Hall 1997, Irlandi et al. 2004, Thomsen 2004) – factors not measured here (but see Chapter 6 for effect of grazing on drift seaweeds). In addition, there were no effect of mussels on *Ulva*. *Ulva* is typically a fast-growing seaweed, particularly under high nutrient levels (Lapointe and Tenore 1981, Duke et al. 1989, Geertz-Hansen et al. 1993). I therefore expected that mussels, through bio-deposition of waste products, would facilitate *Ulva*, as shown in aquaculture studies of bivalves and other organisms (Shpigel et al. 1993, Chopin et al. 2001, Zertuche-González et al. 2009, Liu et al. 2010). However, high abundances of grazing snails and physical abrasion of *Ulva* fronds could also have reduced seaweed biomass and thereby countered any potential smaller facilitative effects from mussels (Geertz-Hansen et al. 1993, Hyslop and Davies 1998, Giannotti and McGlathery 2001, Thomsen 2004).

Conclusions

Seagrass and larger seaweeds function as typical foundation species in estuaries. Here I documented that seagrass and seaweeds were widely distributed, and commonly co-occur across latitudes, estuaries, elevation, sites, and seasons in the South Island of New Zealand. Seagrass and seaweed both facilitated shell-forming organisms, and in the Avon Heathcote survey, additional positive effects were found when seagrass and seaweed co-occurred. In these seagrass beds, shell-formers, particularly mobile trochid snails, were five times more abundant under high densities of *Ulva*, than without the seaweed. In addition, seagrass below ground biomass was facilitated by mussels, but only if the seagrass was not physically disturbed. Furthermore, both above and below ground seagrass biomass were inhibited by high *Ulva*-densities. Finally, I found that *Ulva* entrained drifting seagrass leaves, roots, and rhizomes, potentially facilitating dispersal and establishment of new seagrass patches. This

study shows that interactions between estuarine foundation species can be both positive and negative depending on environmental conditions and focal taxa.

Tables

Table 0.1 ANOVA testing for effects of latitudinal region (north, central, south) and estuaries (15) on arcsine square-root transformed percent cover of (A) seagrass and (B) seaweed (n = 90, except one estuary were n = 76). Alpha was reduced to 0.01 because variances could not be transformed to homogeneity. Significant effects are in bold.

Measure	Test Factor	Df	SS	F-value	p
(A) Seagrass Cover	**Region**	**2**	**1.84**	**8.372**	**<0.001**
	Estuary	**12**	**23.76**	**18.061**	**<0.001**
	Residuals	1321	144.82		
(B) Seaweed Cover	**Region**	**2**	**3.75**	**42.68**	**<0.001**
	Estuary	**12**	**27.08**	**51.43**	**<0.001**
	Residuals	1321	57.96		

Table 0.2 ANOVA testing for effects of year (2014/15 vs 2015/16), season (summer vs. winter), and site (Plover vs. Tern street) on arcsine square-root transformed percent covers of (A) seagrass and (B) seaweed in the Avon-Heathcote Estuary. Alpha was reduced to 0.01 because variances could not be transformed to homogeneity. Significant effects are in bold.

Measure	Test Factor	Df	SS	F-value	p
(A) Seagrass Cover	**Year**	**1**	**3.96**	**49.746**	**<0.001**
	Season	1	0.00	0.007	0.934
	Site	1	0.49	6.166	0.013
	Year×Season	1	0.27	3.341	0.068
	Year×Site	1	0.00	0.008	0.929
	Season×Site	1	0.01	0.179	0.673
	Year×Season×Site	1	0.15	1.893	0.169
(B) Seaweed Cover	**Year**	**1**	**1.979**	**62.700**	**<0.001**
	Season	**1**	**4.239**	**134.306**	**<0.001**
	Site	**1**	**0.943**	**29.878**	**<0.001**
	Year×Season	**1**	**0.730**	**23.130**	**<0.001**
	Year×Site	1	0.027	0.855	0.355
	Season×Site	1	0.068	2.156	0.142
	Year×Season×Site	1	0.007	0.229	0.632
	Residuals	985	31.085		

Table 0.3 ANOVA testing for effects of latitudinal region (north, central, south), estuary (15), elevation (intertidal, subtidal) seagrass (presence-absence) and seaweed (presence-absence) on (A) density (log 10+1 transformed) and (B) richness of shell-forming bivalves and snails in sediment cores (9 cm diameter × 10 cm depth, n = 3). Significant effects are in bold.

Measure	Test Factor	Df	SS	F-value	p
(A) Density	**Region**	**2**	**60.83**	**113.979**	**<0.001**
	Estuary	**12**	**149.57**	**46.711**	**<0.001**
	Elevation	1	0.27	0.994	0.320
	Seagrass	**1**	**16.92**	**63.392**	**<0.001**
	Seaweed	**1**	**8.53**	**31.975**	**<0.001**
	Region×Elevation	2	0.04	0.082	0.921
	Estuary×Elevation	**12**	**8.68**	**2.710**	**0.002**
	Region×Seagrass	**2**	**3.87**	**7.259**	**0.001**
	Estuary×Seagrass	**12**	**14.81**	**4.624**	**<0.001**
	Elevation×Seagrass	1	0.00	0.011	0.915
	Region×Seaweed	2	0.12	0.216	0.806
	Estuary×Seaweed	**12**	**6.69**	**2.090**	**0.018**
	Elevation×Seaweed	1	0.47	1.752	0.187
	Seagrass×Seaweed	1	0.30	1.123	0.290
	Region×Elevation×Seagrass	2	0.99	1.859	0.158
	Estuary×Elevation×Seagrass	**12**	**5.99**	**1.870**	**0.038**
	Region×Elevation×Seaweed	2	0.47	0.882	0.415
	Estuary×Elevation×Seaweed	**11**	**7.44**	**2.536**	**0.005**
	Region×Seagrass×Seaweed	2	0.27	0.502	0.606
	Estuary×Seagrass×Seaweed	**10**	**7.26**	**2.722**	**0.003**
	Elevation×Seagrass×Seaweed	1	0.37	1.393	0.239
	Region×Elevation×Seagrass×Seaweed	2	0.51	0.949	0.388
	Estuary×Elevation×Seagrass×Seaweed	**8**	**8.35**	**3.909**	**<0.001**
	Residuals	267	71.24		
(B) Richness	**Region**	**2**	**260.6**	**98.992**	**<0.001**
	Estuary	**12**	**234.2**	**14.828**	**<0.001**
	Elevation	1	0.1	0.043	0.837
	Seagrass	**1**	**29.2**	**22.223**	**<0.001**
	Seaweed	**1**	**36.5**	**27.747**	**<0.001**
	Region×Elevation	2	1.2	0.451	0.637
	Estuary×Elevation	**12**	**39.9**	**2.529**	**0.004**
	Region×Seagrass	2	1.8	0.678	0.508
	Estuary×Seagrass	12	16.5	1.044	0.408
	Elevation×Seagrass	1	1.8	1.340	0.248
	Region×Seaweed	2	1.8	0.683	0.506
	Estuary×Seaweed	12	14.9	0.945	0.503
	Elevation×Seaweed	1	0.8	0.572	0.450
	Seagrass×Seaweed	1	3.3	2.522	0.113
	Region×Elevation×Seagrass	2	2.5	0.968	0.381
	Estuary×Elevation×Seagrass	12	20.2	1.277	0.232

Region×Elevation×Seaweed	2	2.0	0.769	0.465
Estuary×Elevation×Seaweed	11	13.8	0.950	0.492
Region×Seagrass×Seaweed	2	0.6	0.212	0.809
Estuary×Seagrass×Seaweed	10	9.8	0.748	0.679
Elevation×Seagrass×Seaweed	1	0.0	0.000	0.994
Region×Elevation×Seagrass×Seaweed	2	1.9	0.721	0.487
Estuary×Elevation×Seagrass×Seaweed	8	12.6	1.196	0.301
Residuals	267	351.4		

Table 0.4 ANOVA testing for effects of year (2014/15 vs 2015/16), season (summer vs. winter), and site (Plover vs. Tern street) on (A) density (log 10+1 transformed) and (B) richness of shell forming snails and bivalves, in the Avon-Heathcote Estuary in sediment cores (9 cm diameter × 10 cm depth, n = 4). Significant effects are in bold. Significant effects are in bold.

Measure	Test Factor	Df	SS	F-value	p
(A) Density	**Year**	**1**	**7.99**	**21.035**	**<0.001**
	Season	**1**	**9.72**	**25.570**	**<0.001**
	Site	1	0.41	1.068	0.303
	Elevation	**1**	**2.04**	**5.356**	**0.022**
	Seagrass	**1**	**36.31**	**95.543**	**<0.001**
	Seaweed	**1**	**37.83**	**99.548**	**<0.001**
	Year×Season	**1**	**2.42**	**6.372**	**0.012**
	Year×Site	1	0.19	0.506	0.478
	Season×Site	1	1.08	2.853	0.093
	Year×Elevation	1	0.85	2.226	0.137
	Season×Elevation	1	0.53	1.385	0.241
	Site×Elevation	**1**	**1.91**	**5.031**	**0.026**
	Year×Seagrass	**1**	**4.38**	**11.528**	**0.001**
	Season×Seagrass	1	0.66	1.732	0.190
	Site×Seagrass	1	0.88	2.305	0.131
	Elevation×Seagrass	1	0.01	0.028	0.867
	Year×Seaweed	1	0.23	0.611	0.436
	Season×Seaweed	1	1.27	3.336	0.069
	Site×Seaweed	1	0.10	0.255	0.614
	Elevation×Seaweed	1	0.19	0.505	0.478
	Seagrass×Seaweed	**1**	**7.50**	**19.739**	**<0.001**
	Year×Season×Site	**1**	**2.46**	**6.464**	**0.012**
	Year×Season×Elevation	**1**	**2.51**	**6.617**	**0.011**
	Year×Site×Elevation	1	0.47	1.227	0.269
	Season×Site×Elevation	1	0.04	0.101	0.751
	Year×Season×Seagrass	**1**	**4.09**	**10.772**	**0.001**
	Year×Site×Seagrass	1	0.24	0.625	0.430
	Season×Site×Seagrass	**1**	**2.89**	**7.602**	**0.006**
	Year×Elevation×Seagrass	1	0.46	1.220	0.271
	Season×Elevation×Seagrass	1	0.04	0.106	0.745
	Site×Elevation×Seagrass	1	0.94	2.481	0.117
	Year×Season×Seaweed	1	0.44	1.150	0.285
	Year×Site×Seaweed	1	0.31	0.808	0.370
	Season×Site×Seaweed	**1**	**2.03**	**5.348**	**0.022**
	Year×Elevation×Seaweed	1	0.00	0.010	0.920
	Season×Elevation×Seaweed	1	0.31	0.815	0.368
	Site×Elevation×Seaweed	1	0.00	0.001	0.975
	Year×Seagrass×Seaweed	1	0.04	0.114	0.736
	Season×Seagrass×Seaweed	1	1.46	3.837	0.052
	Site×Seagrass×Seaweed	1	0.37	0.974	0.325

	Elevation×Seagrass×Seaweed	1	0.56	1.470	0.227
	Year×Season×Site×Elevation	1	0.97	2.565	0.111
	Year×Season×Site×Seagrass	**1**	**2.65**	**6.980**	**0.009**
	Year×Season×Elevation×Seagrass	1	1.23	3.225	0.074
	Year×Site×Elevation×Seagrass	1	0.02	0.043	0.835
	Season×Site×Elevation×Seagrass	1	0.06	0.153	0.696
	Year×Season×Site×Seaweed	**1**	**2.36**	**6.214**	**0.014**
	Year×Season×Elevation×Seaweed	1	0.19	0.497	0.482
	Year×Site×Elevation×Seaweed	1	0.55	1.437	0.232
	Season×Site×Elevation×Seaweed	1	0.03	0.085	0.771
	Year×Season×Seagrass×Seaweed	1	0.05	0.133	0.716
	Year×Site×Seagrass×Seaweed	1	0.12	0.304	0.582
	Season×Site×Seagrass×Seaweed	1	1.32	3.470	0.064
	Year×Elevation×Seagrass×Seaweed	1	0.22	0.572	0.450
	Season×Elevation×Seagrass×Seaweed	1	0.07	0.186	0.667
	Site×Elevation×Seagrass×Seaweed	1	0.00	0.001	0.977
	Year×Season×Site×Elevation×Seagrass	1	0.43	1.121	0.291
	Year×Season×Site×Elevation×Seaweed	**1**	**1.52**	**4.001**	**0.047**
	Year×Season×Site×Seagrass×Seaweed	1	0.97	2.563	0.111
	Year×Season×Elevation×Seagrass×Seaweed	1	0.16	0.412	0.522
	Year×Site×Elevation×Seagrass×Seaweed	1	0.01	0.014	0.907
	Season×Site×Elevation×Seagrass×Seaweed	1	0.01	0.021	0.884
	Year×Season×Site×Elevation×Seagrass×Seaweed	1	0.83	2.193	0.140
	Residuals	189	71.82		
(B) Richness	**Year**	**1**	**76.3**	**43.089**	**<0.001**
	Season	**1**	**9.3**	**5.249**	**0.023**
	Site	**1**	**28.1**	**15.900**	**<0.001**
	Elevation	1	4.4	2.491	0.116
	Seagrass	**1**	**16.1**	**9.096**	**0.003**
	Seaweed	**1**	**27.5**	**15.547**	**<0.001**
	Year×Season	**1**	**42.2**	**23.856**	**<0.001**
	Year×Site	1	0.1	0.081	0.777
	Season×Site	1	4.2	2.369	0.125
	Year×Elevation	**1**	**11.5**	**6.506**	**0.012**
	Season×Elevation	1	1.5	0.830	0.363
	Site×Elevation	**1**	**28.8**	**16.258**	**<0.001**
	Year×Seagrass	1	4.2	2.347	0.127
	Season×Seagrass	**1**	**4.9**	**2.742**	**0.099**
	Site×Seagrass	1	2.5	1.397	0.239
	Elevation×Seagrass	1	0.9	0.482	0.489
	Year×Seaweed	1	2.5	1.413	0.236
	Season×Seaweed	1	0.6	0.342	0.560
	Site×Seaweed	1	0.1	0.066	0.798
	Elevation×Seaweed	1	4.4	2.511	0.115
	Seagrass×Seaweed	**1**	**7.7**	**4.341**	**0.039**
	Year×Season×Site	1	2.6	1.448	0.230

Year×Season×Elevation	1	5.8	3.266	0.072
Year×Site×Elevation	**1**	**21.0**	**11.851**	**0.001**
Season×Site×Elevation	1	3.3	1.866	0.174
Year×Season×Seagrass	1	0.2	0.118	0.731
Year×Site×Seagrass	1	0.2	0.130	0.719
Season×Site×Seagrass	1	0.2	0.120	0.729
Year×Elevation×Seagrass	1	3.0	1.719	0.191
Season×Elevation×Seagrass	1	1.1	0.626	0.430
Site×Elevation×Seagrass	1	0.2	0.136	0.713
Year×Season×Seaweed	1	1.7	0.980	0.324
Year×Site×Seaweed	1	0.0	0.000	0.992
Season×Site×Seaweed	1	1.2	0.664	0.416
Year×Elevation×Seaweed	1	1.0	0.550	0.459
Season×Elevation×Seaweed	1	0.7	0.401	0.528
Site×Elevation×Seaweed	1	0.3	0.150	0.699
Year×Seagrass×Seaweed	1	4.5	2.549	0.112
Season×Seagrass×Seaweed	1	0.6	0.356	0.552
Site×Seagrass×Seaweed	1	0.0	0.006	0.938
Elevation×Seagrass×Seaweed	1	0.0	0.006	0.937
Year×Season×Site×Elevation	1	0.9	0.520	0.472
Year×Season×Site×Seagrass	**1**	**7.2**	**4.055**	**0.045**
Year×Season×Elevation×Seagrass	1	6.6	3.733	0.055
Year×Site×Elevation×Seagrass	1	1.6	0.916	0.340
Season×Site×Elevation×Seagrass	1	2.8	1.599	0.208
Year×Season×Site×Seaweed	1	0.2	0.114	0.736
Year×Season×Elevation×Seaweed	1	3.9	2.192	0.140
Year×Site×Elevation×Seaweed	1	0.0	0.003	0.960
Season×Site×Elevation×Seaweed	1	2.3	1.316	0.253
Year×Season×Seagrass×Seaweed	1	0.3	0.197	0.657
Year×Site×Seagrass×Seaweed	1	0.0	0.002	0.961
Season×Site×Seagrass×Seaweed	**1**	**7.2**	**4.053**	**0.046**
Year×Elevation×Seagrass×Seaweed	1	3.4	1.948	0.164
Season×Elevation×Seagrass×Seaweed	1	1.5	0.854	0.357
Site×Elevation×Seagrass×Seaweed	1	0.0	0.008	0.931
Year×Season×Site×Elevation×Seagrass	1	2.7	1.540	0.216
Year×Season×Site×Elevation×Seaweed	1	0.1	0.064	0.800
Year×Season×Site×Seagrass×Seaweed	1	0.0	0.001	0.979
Year×Season×Elevation×Seagrass×Seaweed	1	0.0	0.027	0.871
Year×Site×Elevation×Seagrass×Seaweed	1	0.8	0.443	0.506
Season×Site×Elevation×Seagrass×Seaweed	1	0.1	0.048	0.826
Year×Season×Site×Elevation×Seagrass×Seaweed	1	5.0	2.802	0.096
Residuals	189	334.5		

Table 0.5 Experiment 1. ANOVA testing for effect of manipulated amounts of seagrass (control, cut, removed), mussels (adding 0, 1, 4), and *Ulva* seaweed (adding 0, 150, 500 mL) on (A) density and (B) richness of shell forming snails and bivalves in the Avon-Heathcote Estuary in sediment cores (9 cm diameter × 10 cm depth, n = 4). Significant effects are in bold.

Measure	Test Factor	Df	SS	F-value	p
(A) Density	Seagrass	2	26840000	0.170	0.844
	Mussel	2	60940000	0.386	0.681
	Seaweed	**2**	**5914000000**	**37.424**	**<0.001**
	Seagrass×Mussel	4	413100000	1.307	0.274
	Seagrass×Seaweed	4	241800000	0.765	0.551
	Mussel×Seaweed	4	269800000	0.854	0.495
	Seagrass×Mussel×Seaweed	8	939900000	1.487	0.175
	Residuals	81	6400000000		
(B) Richness	Seagrass	2	0.69	0.321	0.726
	Mussel	**2**	**7.35**	**3.442**	**0.037**
	Seaweed	2	1.46	0.685	0.507
	Seagrass×Mussel	4	1.20	0.282	0.889
	Seagrass×Seaweed	4	6.76	1.582	0.187
	Mussel×Seaweed	**4**	**15.43**	**3.611**	**0.009**
	Seagrass×Mussel×Seaweed	8	5.02	0.587	0.786
	Residuals	81	86.50		

Table 0.6 Experiment 1. ANOVA testing for effect of manipulated amounts of seagrass (control, cut, removed), mussels (adding 0, 1, 4), and *Ulva* seaweed (adding 0, 150, 500 mL) on (A) seagrass root biomass and (B) seaweed biomass (pooling across the *Ulva* test factor) in the Avon-Heathcote Estuary in sediment cores (9 cm diameter × 10 cm depth, n = 4). Significant effects are in bold.

Measure	Test Factor	Df	SS	F-value	p
(A) Seagrass root biomass	**Seagrass**	**2**	**0.525**	**6.671**	**0.002**
	Mussel	2	0.026	0.335	0.716
	Seaweed	**2**	**0.252**	**3.200**	**0.046**
	Seagrass×Mussel	**4**	**0.508**	**3.227**	**0.017**
	Seagrass×Seaweed	4	0.151	0.960	0.434
	Mussel×Seaweed	4	0.110	0.699	0.595
	Seagrass×Mussel×Seaweed	8	0.404	1.282	0.265
	Residuals	80	3.150		
(B) Seaweed biomass	Seagrass	2	2.06	0.526	0.593
	Mussel	2	1.01	0.259	0.772
	Seagrass×Mussel	4	0.87	0.111	0.978
	Residuals	99	193.86		

Table 0.7 Experiment 2. ANOVA testing for effect of manipulated amounts of seagrass (control, cut, removed) and *Ulva* seaweed (adding 0, 150, 500 mL) on (A) density and (B) richness of shell forming snails and bivalves in the Avon-Heathcote Estuary (n = 3). Significant effects are in bold.

Measure	Test Factor	Df	SS	F-value	p
(A) Density	Seagrass	2	9556506	0.637	0.535
	Seaweed	2	52683217	3.509	0.041
	Seagrass×Seaweed	4	24796624	0.826	0.518
	Residuals	36	270240593		
(B) Richness	**Seagrass**	**2**	**7.600**	**5.436**	**0.009**
	Seaweed	2	2.033	1.454	0.247
	Seagrass×Seaweed	4	2.400	0.858	0.498
	Residuals	36	25.167		

Table 0.8 Experiment 2. ANOVA testing for effect of manipulated amounts of seagrass (control, cut, removed) and *Ulva* seaweed (adding 0, 150, 500 mL) on (A) seagrass leaf biomass (only for the control seagrass plots), (B) seagrass root biomass and (C) seaweed biomass (pooling across the *Ulva* test factor) in the Avon-Heathcote Estuary (n = 3). Significant effects are in bold.

Measure	Test Factor	Df	SS	F-value	p
(A) Seagrass leaf biomass	**Seaweed**	**2**	**0.366**	**9.380**	**0.014**
	Residuals	6	0.039		
(B) Seagrass root biomass	Seagrass	2	0.004	0.050	0.951
	Seaweed	**2**	**0.444**	**6.115**	**0.009**
	Seagrass×Seaweed	4	0.208	1.434	0.263
	Residuals	18	0.654		
(C) Seaweed biomass	Seagrass	2	1.793	0.636	0.543
	Residuals	15	21.146		

Figures

Figure 0.1 Map of sampled estuaries around the South Island of New Zealand, from a latitudinal survey (left, middle), and a temporal survey in the Avon-Heathcote Estuary.

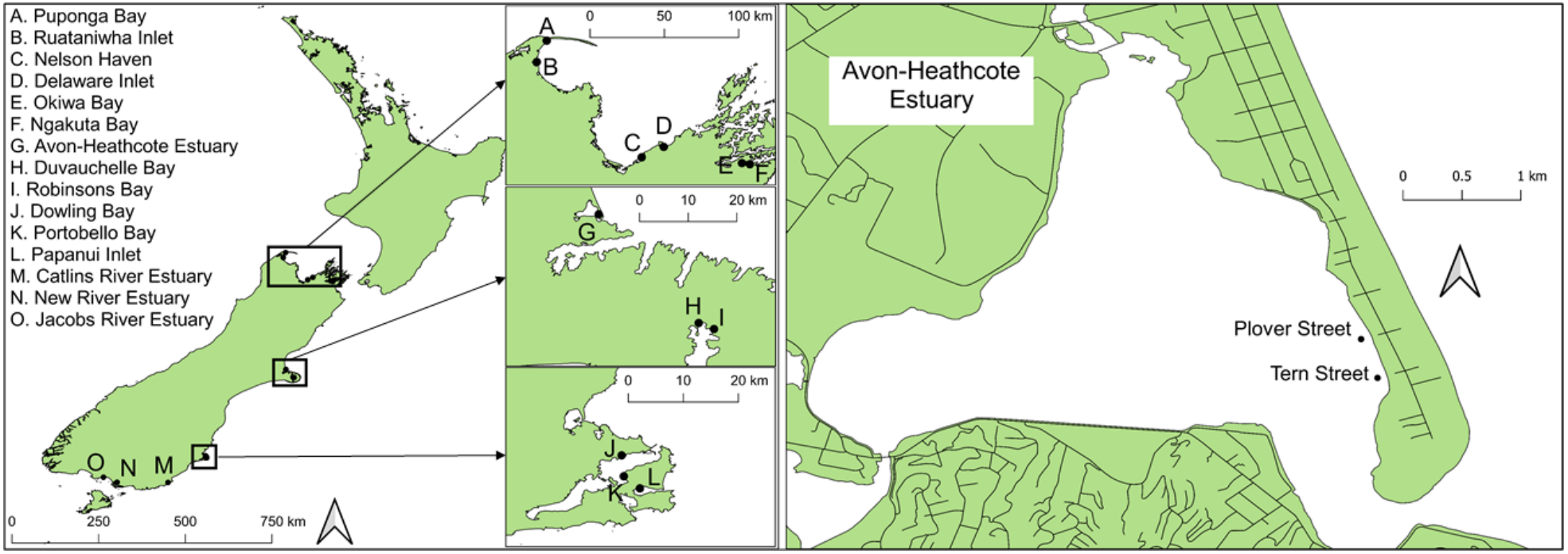


Figure 0.2 Percent cover of seagrass vs. seaweed from a latitudinal survey from 15 estuaries on the South Island of New Zealand. There was a significant negative relationship between cover of seagrass and seaweed. White, grey and black symbols represent northern, central estuaries, and southern estuaries, respectively. 343 (25%) of all samples had co-occurring seagrass and seaweed, 500 (37%) had only seagrass, 316 (23%) only seaweed, and 177 (13%) neither seagrass or seaweed.

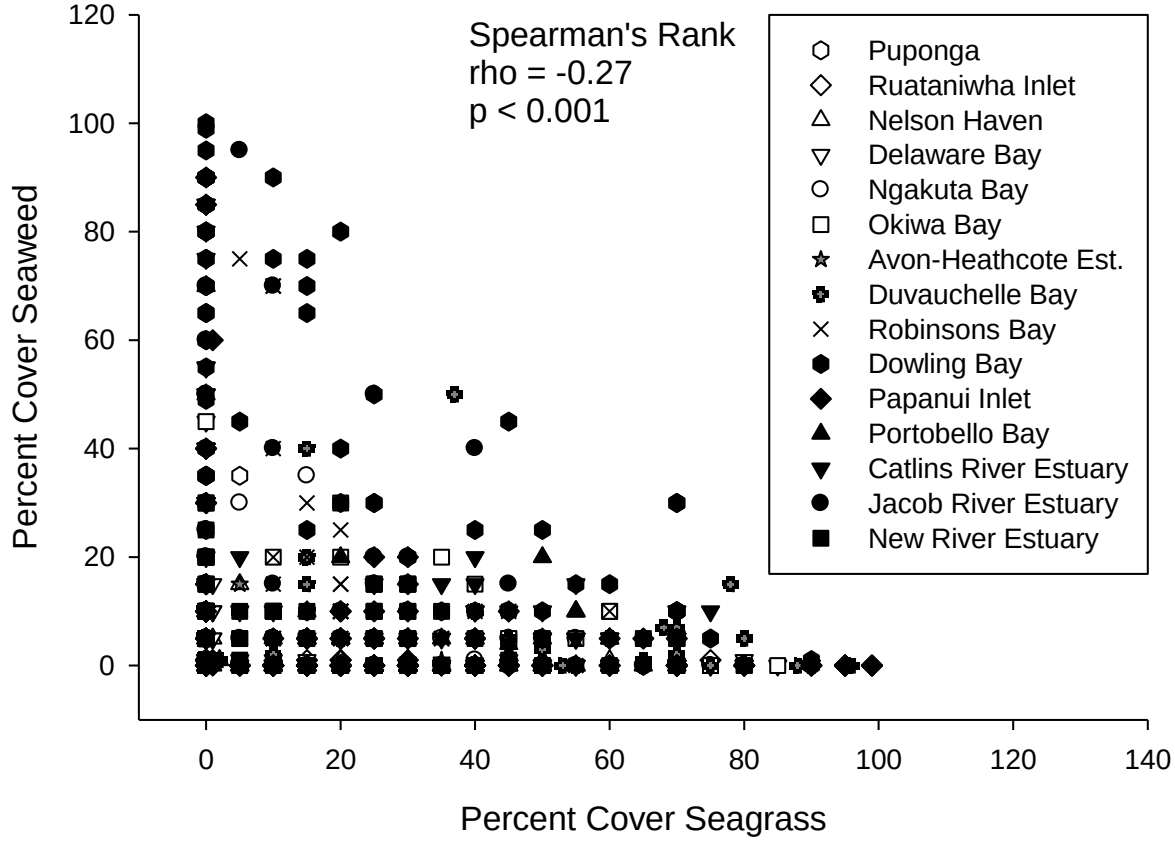


Figure 0.3 Percent cover (mean ± SE) of seagrass, seaweed, dead shells, bare sediment and rocks in 15 estuaries from three latitudinal regions around the South Island of New Zealand (see Figure 1.1 for names of estuaries).

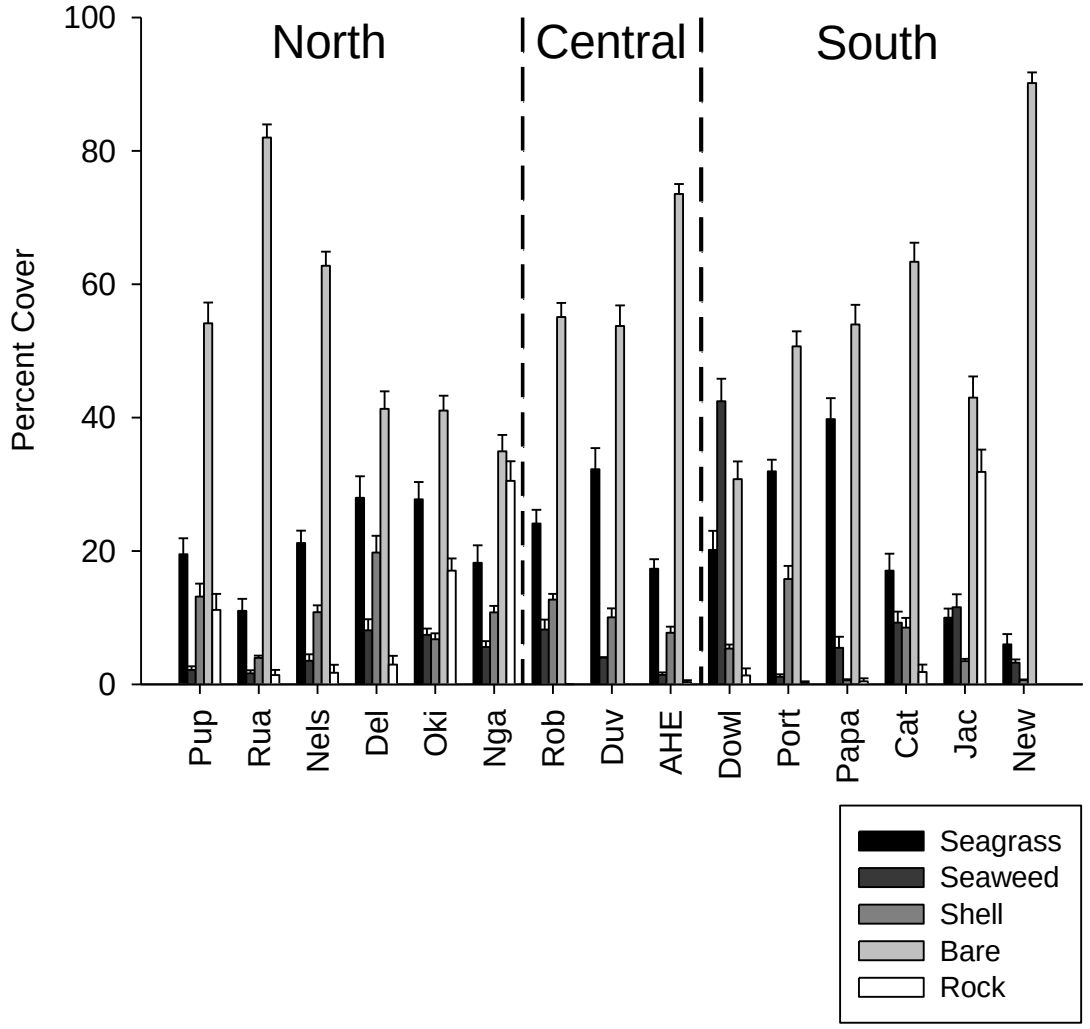


Figure 0.4 Percent cover of seagrass vs. seaweed from a seasonal survey in the Avon-Heathcote Estuary. There was a significant negative relationship between cover of seagrass and seaweed. White and black symbols represent Plover and Tern street samples, respectively. 618 (62%) of all samples had co-occurring seagrass and seaweed, 124 (12%) had only seagrass, 187 (19%) only seaweed, and 64 (6%) neither seagrass or seaweed.

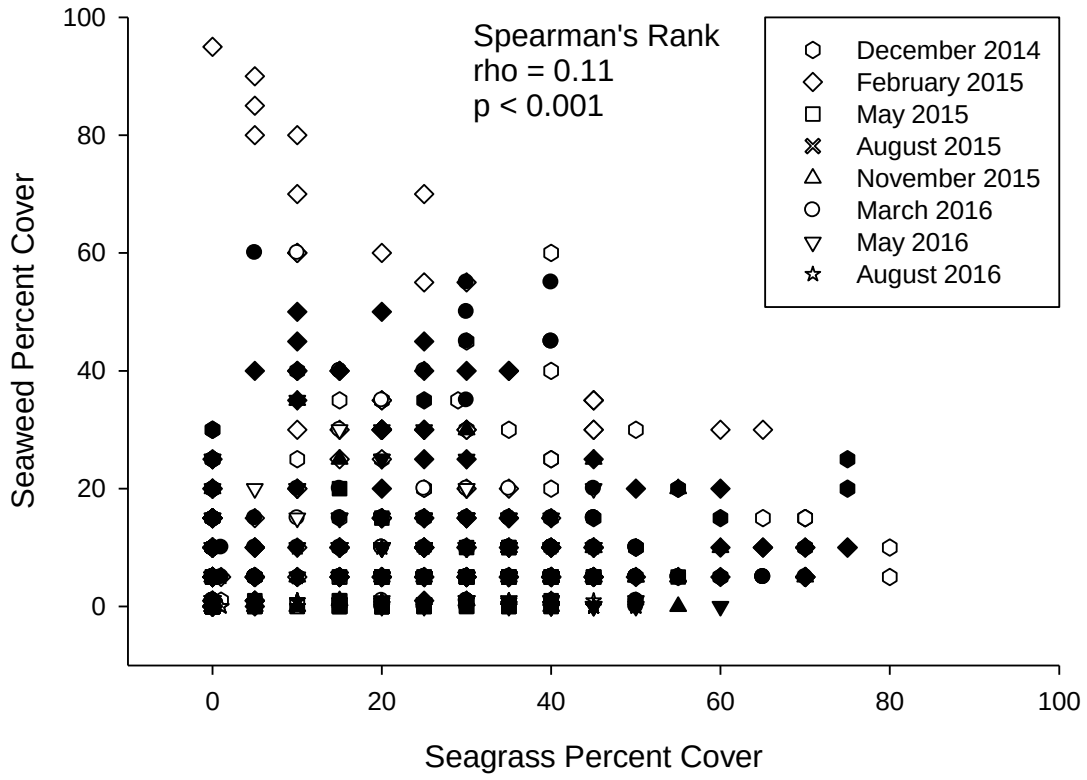


Figure 0.5 Percent cover (+ SE) of seagrass, seaweed, dead shells, bare sediment, and rocks at (A) Tern Street and (B) Plover Street, in early/late summer (December-March) and winter (May-August) from 2014 to 2016 in the Avon-Heathcote Estuary (data for August 2015 (both sites) and November 2015 (Plover only) were lost).

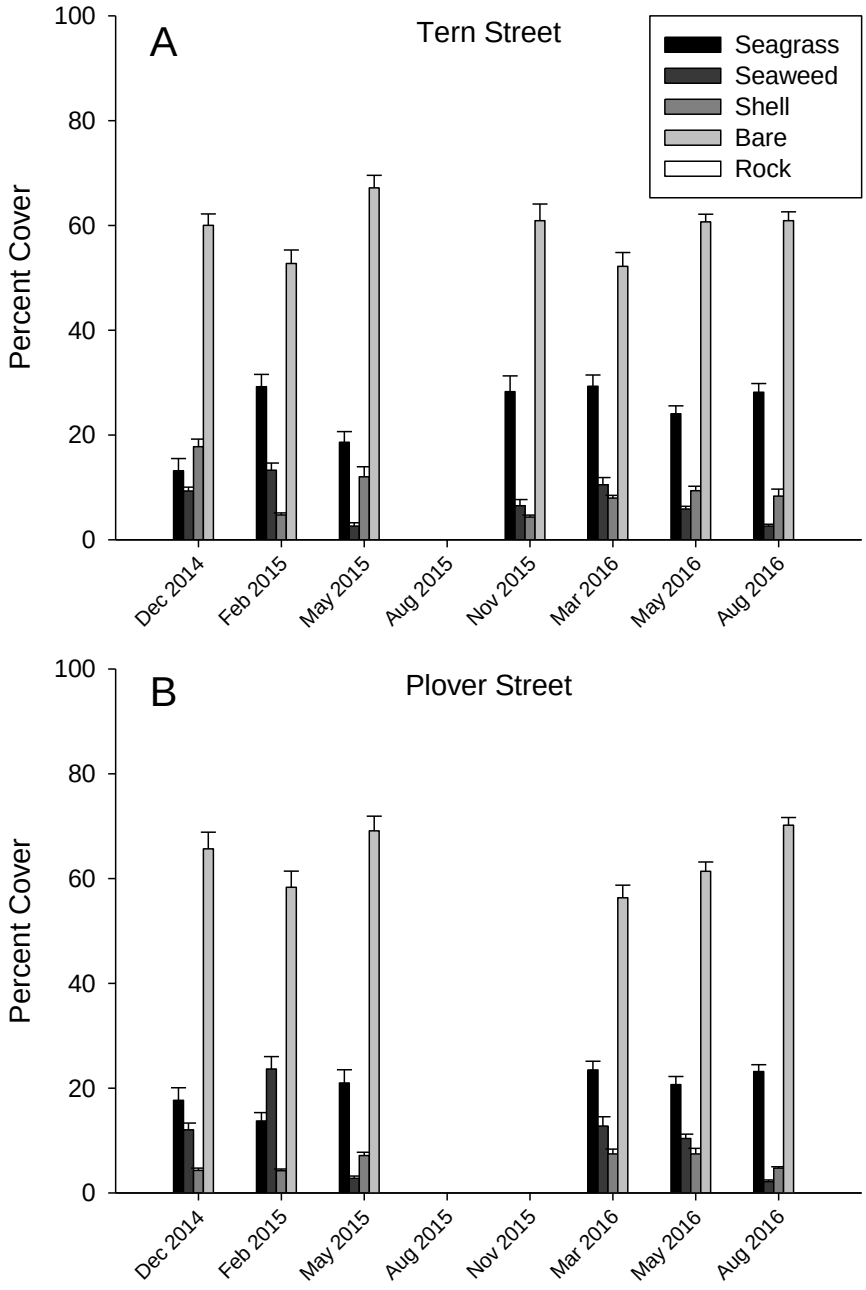


Figure 0.6 (A) Percent composition of shell-forming taxa (snails, bivalves) from all samples taken from an estuary. (B) Shell-former density (+SE) and (C) taxonomic richness in each sampled habitat treatment from each estuary. Estuary names relate to those in Figure 1. The first 6 estuaries (Pup to Nga) are northern, central estuaries are Rob to AHE, and the last 5 (Dowl to New) are southern.

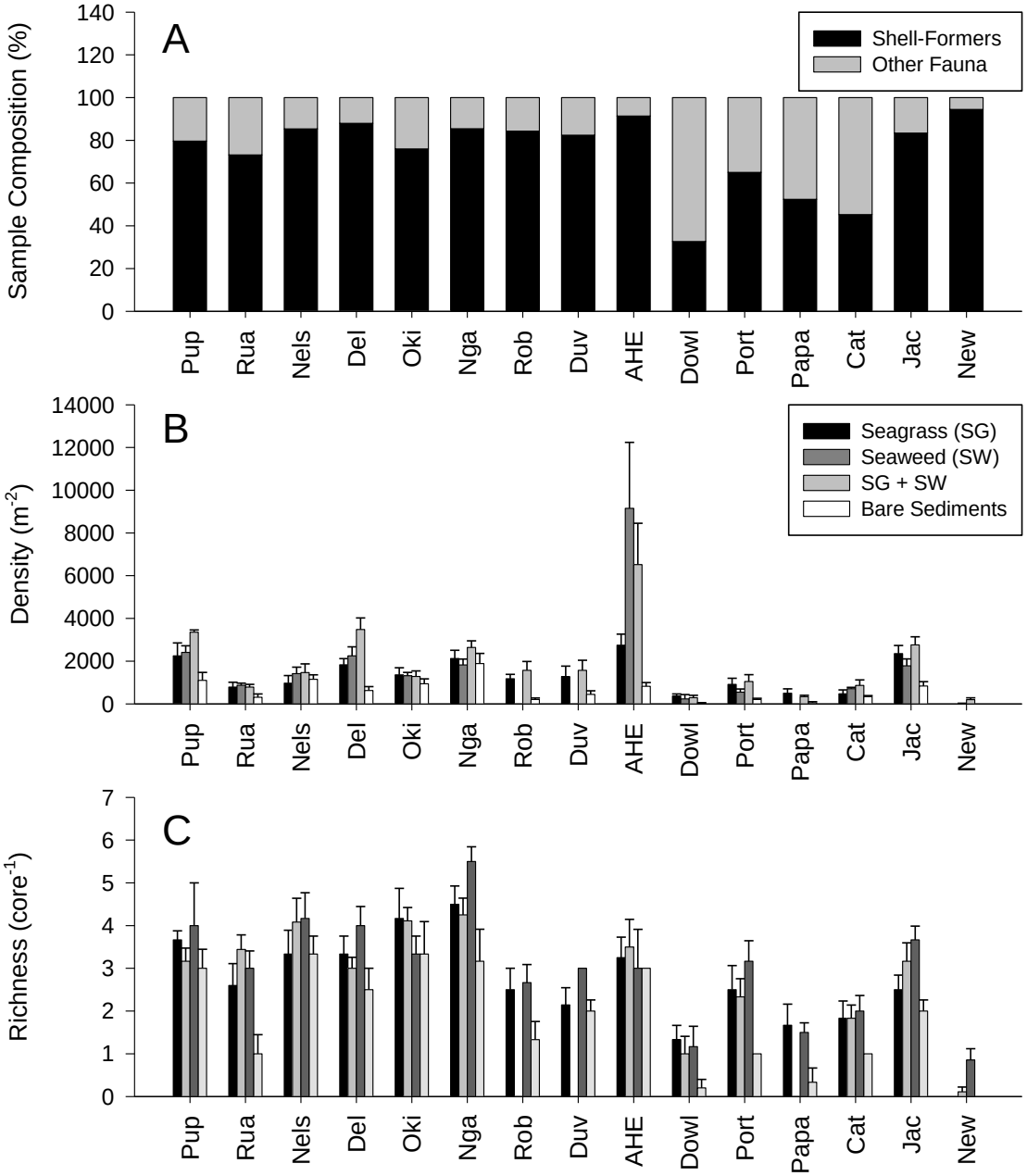


Figure 0.7 Densities (+SE) of shell-forming snails and bivalves from sediment cores in the Avon-Heathcote Estuary pooled across (A) Year (2015 vs 2016), (B) Season (summer vs winter), (C) Site (Plover vs Tern Street), (D) Elevation (subtidal vs intertidal), and (E) Habitat (Seagrass, Seaweed, Seagrass+Seaweed (SG+SW), and Bare sediments).

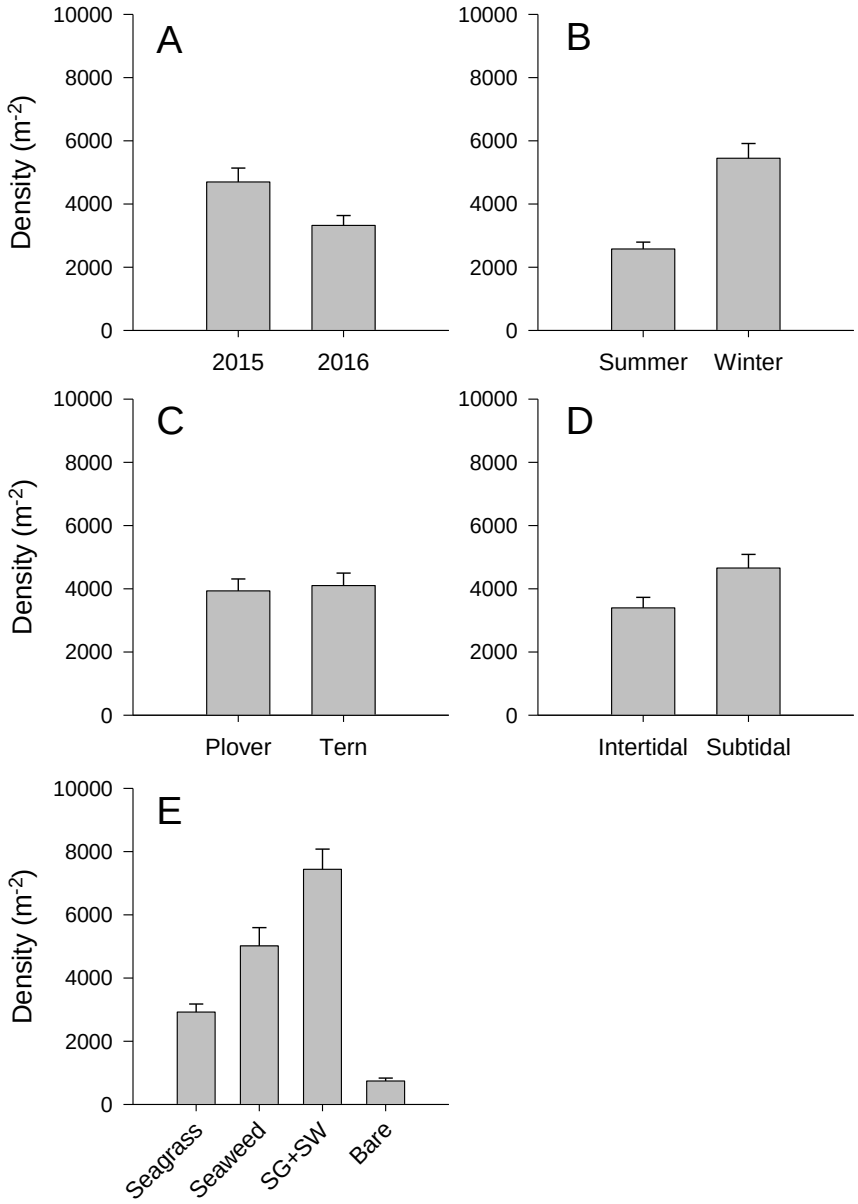


Figure 0.8 Taxonomic richness (+SE) of shell-forming invertebrates snails and bivalves from sediment cores in the Avon-Heathcote Estuary pooled across (A) Year (2015 vs 2016), (B) Season (summer vs winter), (C) Site (Plover vs Tern Street), (D) Elevation (subtidal vs intertidal), and (E) Habitat (Seagrass, Seaweed, Seagrass+Seaweed (SG+SW), and Bare sediments).

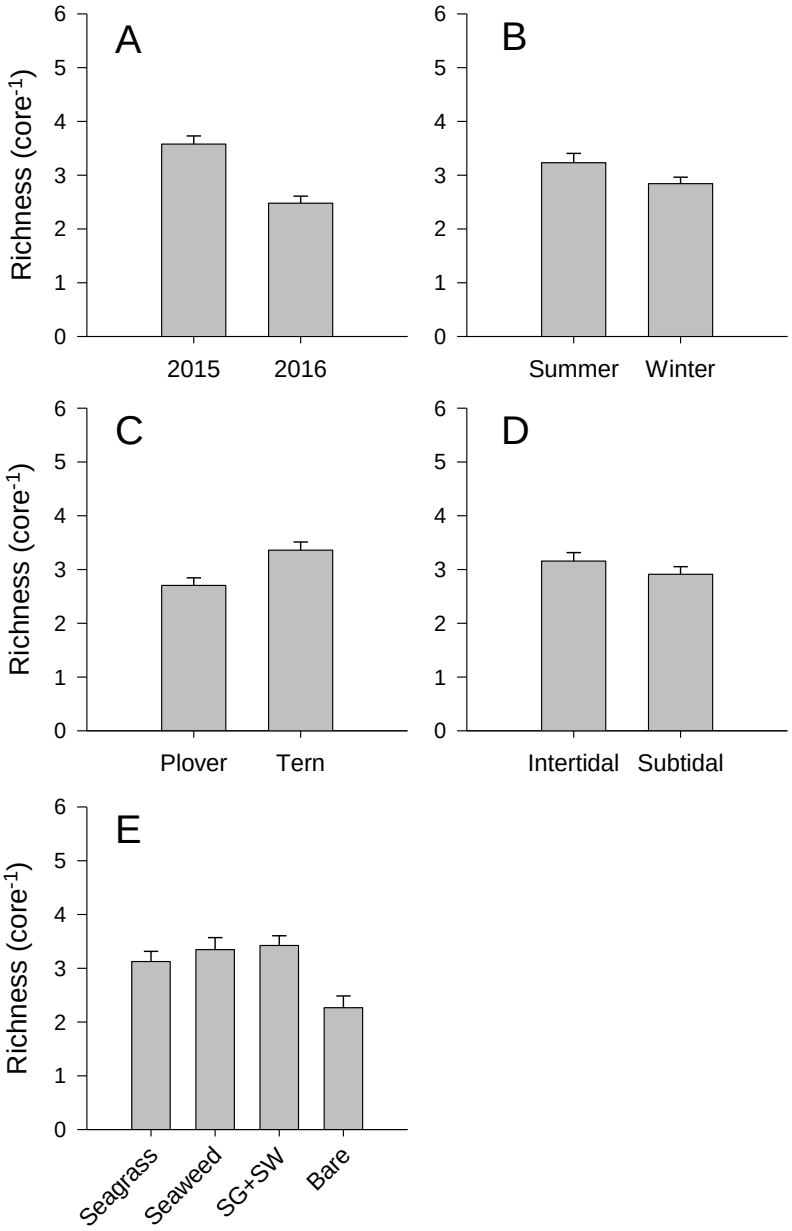


Figure 0.9 Experiment 1. Density (A, C, E) and taxonomic richness (B, D, F) (+SE) of shell-forming snails and bivalves grouped into three levels of seagrass (A, B), mussels (C, D), and *Ulva*-seaweed (E, F) in the Avon-Heathcote Estuary. Samples (n = 36) were collected with a sediment corer (9 cm diameter × 10 cm depth). Removed = seagrass removed by cutting leaves at the sediment surface, Cut = seagrass leaves cut to half their length, Control = undisturbed seagrass control. '+' = the number of mussels added to each plot. 'mL' = volume of wet *Ulva* added to each plot.

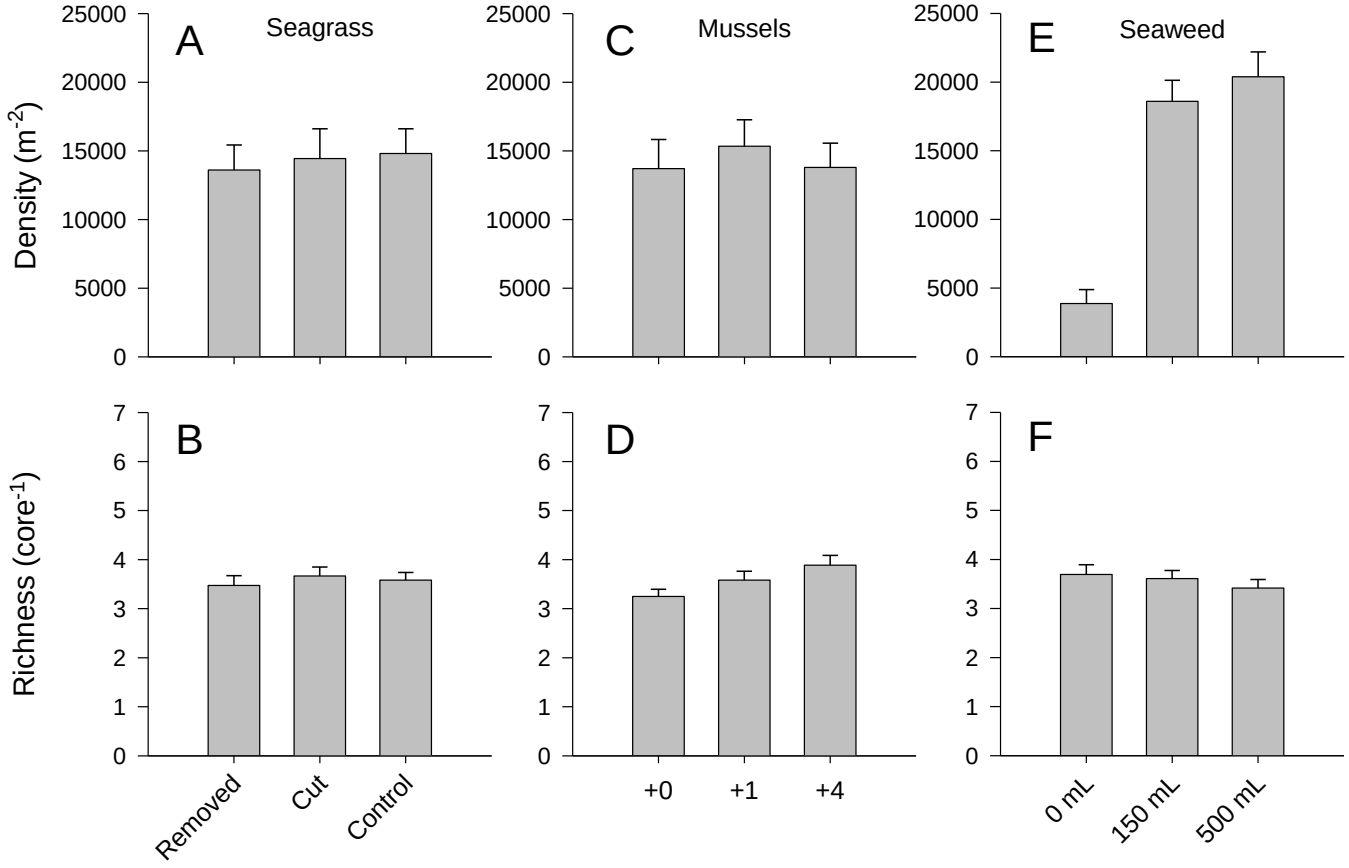


Figure 0.10 Experiment 1. Seagrass root biomass (+SE, grams dry weight) for different levels of (A) seagrass manipulation (control, cut, removed) and mussel addition (0, 1, 4 mussels, *n* = 12) and (B) seaweed additions (0 mL, 150 mL, 500 mL, *n* = 36) in the Avon-Heathcote Estuary. Samples were collected with a sediment corer (9 cm diameter × 10 cm depth).

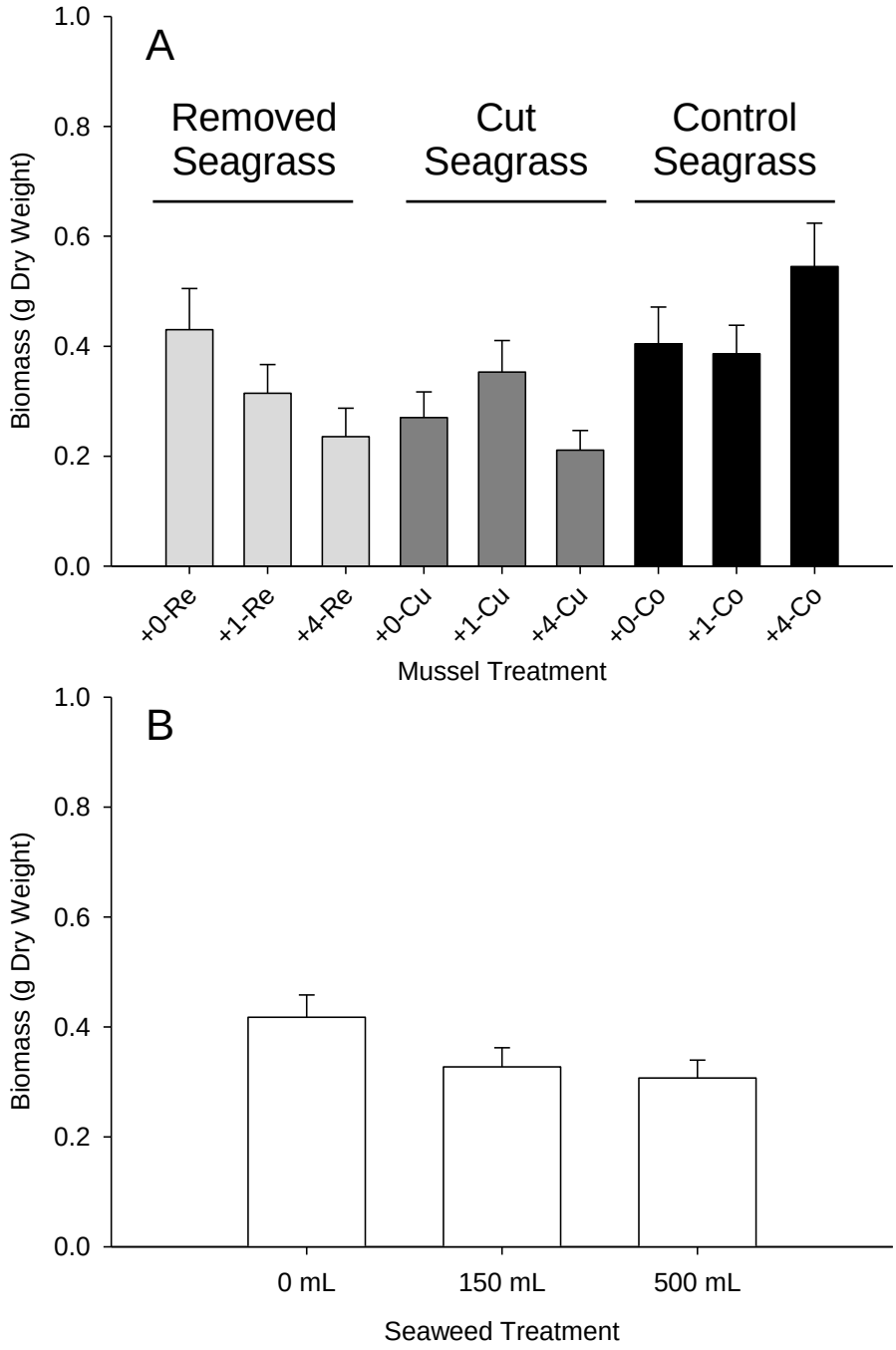


Figure 0.11 Experiment 2. Density (A, C) and taxonomic richness (B, D) (+SE) of shell forming snails and bivalves for different levels of (A, B) seagrass leaves (control, cut, removed, n = 15) and (C, D) *Ulva* seaweed (0, 150, 500 mL wet *Ulva*, n = 9 for 0 mL, n = 18 for others) in the Avon-Heathcote Estuary.

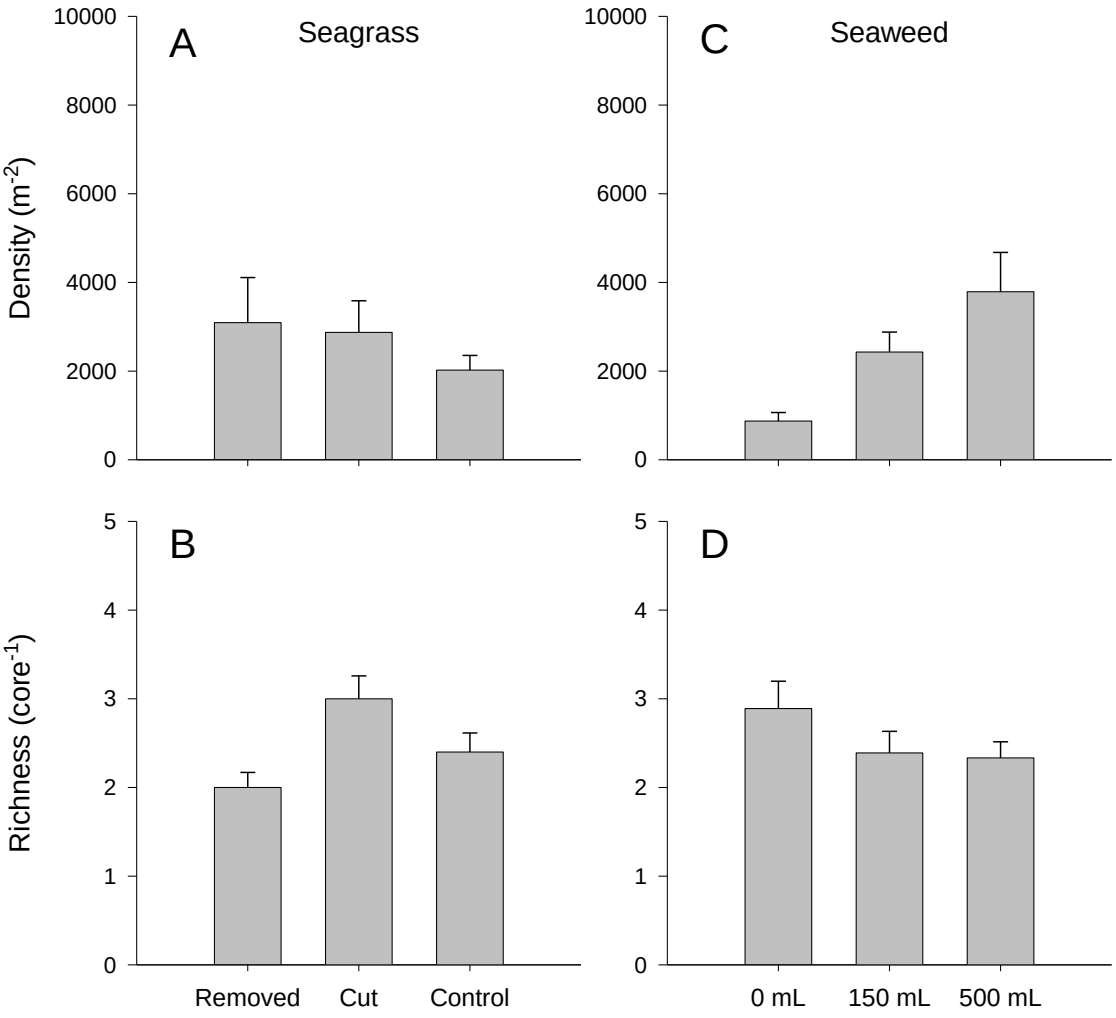
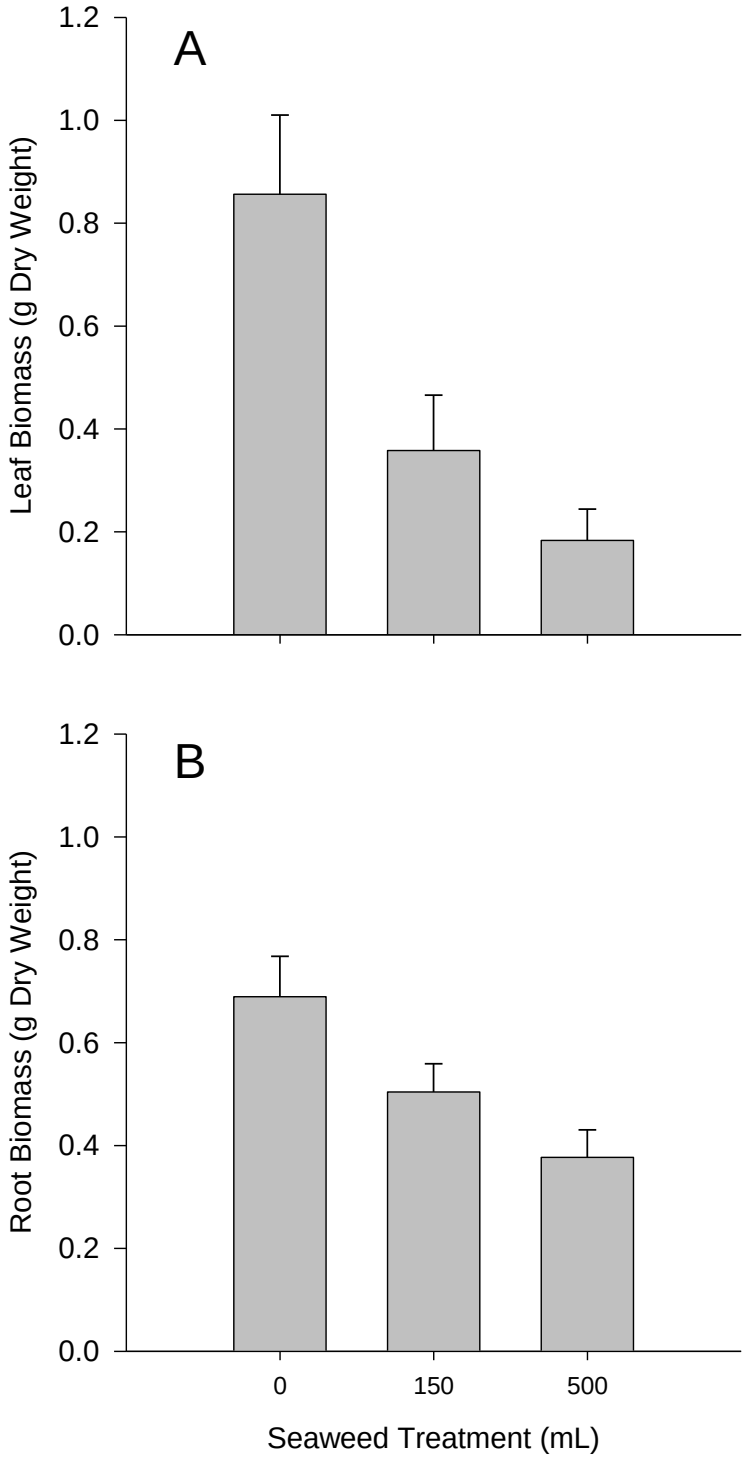


Figure 0.12 Experiment 2. Biomass (+SE) of seagrass (A) above ground leaves (evaluted from undisturbed seagrass 'controls', *n* = 3) and (B) below-ground roots and rhizomes (evaluated across all seagrass treatments, *n* = 9) in the Avon-Heathcote Estuary for three levels of *Ulva* seaweed (0, 150, 500 mL wet volume).



References

Abbe, G. 1988. Population structure of the american oyster, C*rassostrea virginica,* on an oyster bar in central chesapeake bay: changes associated with shell planting and increased recruitment. Journal of Shellfish Research **7**:33-40.

Abrams, M. D., and Scott, M. L. 1989. Disturbance-mediated accelerated succession in two Michigan forest types. Forest Science **35**:42-49.

Abreu, M. H., Pereira, R., Sousa-Pinto, I., and Yarish, C. 2011. Ecophysiological studies of the non-indigenous species G*racilaria vermiculophylla* (Rhodophyta) and its abundance patterns in Ria de Aveiro Lagoon, Portugal. European Journal of Phycology **46**:453-464.

Airoldi, L. 2000. Responses of algae with different life histories to temporal and spatial variability of disturbance in subtidal reefs. Marine Ecology Progress Series **195**:81-92.

Angelini, C., van der Heide, T., Griffin, J. N., Morton, J. P., Derksen-Hooijberg, M., Lamers, L. P., Smolders, A. J., and Silliman, B. R. 2015. Foundation species' overlap enhances biodiversity and multifunctionality from the patch to landscape scale in southeastern United States salt marshes. Proceedings of the Royal Society B **282**:20150421.

Ayres-Peres, L., and Mantelatto, F. L. 2010. Epibiont occurrence on gastropod shells used by the hermit crab *Loxopagurus loxochelis* (Anomura: Diogenidae) on the northern coast of São Paulo, Brazil. Zoologia (Curitiba) **27**:222-227.

Bashan, Y., Salazar, B., Puente, M. E., Bacilio, M., and Linderman, R. 2009. Enhanced establishment and growth of giant cardon cactus in an eroded field in the Sonoran Desert using native legume trees as nurse plants aided by plant growth-promoting microorganisms and compost. Biology and Fertility of Soils **45**:585-594.

Battley, P. F., Melville, D. S., Schuckard, R., and Ballance, P. F. 2011. *Zostera muelleri* as a structuring agent of benthic communities in a large intertidal sandflat in New Zealand. Journal of Sea Research **65**:19-27.

Bell, S. S., Brooks, R. A., Robbins, B. D., Fonseca, M. S., and Hall, M. O. 2001. Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation. Biological Conservation **100**:115-123.

Bell, S. S., and Hall, M. 1997. Drift macroalgal abundance in seagrass beds: Investigating large-scale associations with physical and biotic attributes. Marine Ecology-Progress Series **147**:277.

Bell, S. S., Hall, M. O., and Robbins, B. D. 1995. Toward a landscape approach in seagrass beds: using macroalgal accumulation to address questions of scale. Oecologia **104**:163-168.

Berezina, N., Golubkov, S., and Gubelit, J. 2005. Grazing effects of alien amphipods on macroalgae in the littoral zone of the Neva Estuary (eastern Gulf of Finland, Baltic Sea). Oceanological and Hydrobiological studies **34**:63-82.

Biber, P. D. 2007. Transport and persistence of drifting macroalgae (Rhodophyta) are strongly influenced by flow velocity and substratum complexity in tropical seagrass habitats. Marine Ecology Progress Series **343**:115-122.

Biber, P. D., Kenworthy, W. J., and Paerl, H. W. 2009. Experimental analysis of the response and recovery of *Zostera marina* (l.) and *Halodule wrightii* (Ascher.) to repeated light-limitation stress. Journal of Experimental Marine Biology and Ecology **369**:110-117.

Bologna, P. A., and Heck, K. L. 2000. Impacts of seagrass habitat architecture on bivalve settlement. Estuaries **23**:449-457.

Booth, D. M., and Heck Jr., K. L. 2009. Effects of the american oyster *Crassostrea virginica* on growth rates of the seagrass *Halodule wrightii*. Marine Ecology Progress Series **389**:117-126.

Boström, C., and Bonsdorff, E. 2000. Zoobenthic community establishment and habitat complexity the importance of seagrass shoot-density, morphology and physical disturbance for faunal recruitment. Marine Ecology Progress Series **205**:123-138.

Boström, C., Jackson, E. L., and Simenstad, C. A. 2006. Seagrass landscapes and their effects on associated fauna: a review. Estuarine, Coastal and Shelf Science **68**:383-403.

Brasier, M. D. 1975. An outline history of seagrass communities. Palaeontology **18**:681-702.

Britton-Simmons, K. H., Rhoades, A. L., Pacunski, R. E., Galloway, A. W. E., Lowe, A. T., Sosik, E. A., Dethier, M. N., and Duggins, D. O. 2012. Habitat and bathymetry influence the landscape-scale distribution and abundance of drift macrophytes and associated invertebrates. Limnology and Oceanography **57**:176-184.

Brun, F. G., Hernández, I., Vergara, J. J., and Pérez-Lloréns, J. L. 2003a. Growth, carbon allocation and proteolytic activity in the seagrass *Zostera noltii* shaded by *Ulva* canopies. Functional Plant Biology **30**:551-560.

Brun, F. G., Vergara, J. J., Navarro, G., Hernández, I., and Pérez-Lloréns, J. L. 2003b. Effect of shading by *Ulva rigida* canopies on growth and carbon balance of the seagrass *Zostera noltii*. Marine Ecology Progress Series **265**:85-96.

Cacabelos, E., Engelen, A. H., Mejia, A., and Arenas, F. 2012. Comparison of the assemblage functioning of estuary systems dominated by the seagrass *Nanozostera noltii* versus the invasive drift seaweed *Gracilaria vermiculophylla*. Journal of Sea Research **72**:99-105.

Callaway, R., Desroy, N., Dubois, S. F., Fournier, J., Frost, M., Godet, L., Hendrick, V. J., and Rabaut, M. 2010. Ephemeral bio-engineers or reef-building polychaetes: How stable are aggregations of the tube worm *Lanice conchilega* (Pallas, 1766)? Integrative and Comparative Biology **50**:237-250.

Carson, S., and Morris, R. 2017. Field guide to the New Zealand seashore. HarperCollins Publishers, Auckland, New Zealand.

Chapman, A. R. O. 1981. Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margaret's Bay, eastern Canada. Marine Biology **62**:307-311.

Chesson, P. L. 1985. Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. Theoretical Population Biology **28**:263-287.

Chopin, T., Buschmann, A. H., Halling, C., Troell, M., Kautsky, N., Neori, A., Kraemer, G. P., Zertuche-González, J. A., Yarish, C., and Neefus, C. 2001. Integrating seaweeds into marine aquaculture systems: a key toward sustainability. Journal of Phycology **37**:975-986.

Coates, K. D., Emmingham, W. H., and Radosevich, S. R. 1991. Conifer-seedling success and microclimate at different levels of herb and shrub cover in a *Rhododendron–Vaccinium–Menziesia* community of south central British Columbia. Canadian Journal of Forest Research **21**:858-866.

Coffaro, G., and Bocci, M. 1997. Resources competition between *Ulva rigida* and *Zostera marina*: a quantitative approach applied to the Lagoon of Venice. Ecological Modelling **102**:81-95.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology **42**:710-723.

Connolly, R. M., and Hindell, J. S. 2006. Review of nekton patterns and ecological processes in seagrass landscapes. Estuarine, Coastal and Shelf Science **68**:433-444.

Cummins, S., Roberts, D., and Zimmerman, K. 2004. Effects of the green macroalga *Enteromorpha intestinalis* on macrobenthic and seagrass assemblages in a shallow coastal estuary. Marine Ecology Progress Series **266**:77-87.

Dauer, D., Tourtellotte, G., and Ewing, R. 1982. Oyster shells and artificial worm tubes: The role of refuges in structuring benthic communities of the lower Chesapeake Bay. Internationale Revue der Gesamten Hydrobiologie und Hydrographie **67**:661-677.

Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. Pages 81-96 *in* Proceedings of the colloquium on conservation problems in Antarctica. Allen Press Lawrence, Kansas, USA.

den Hartog, C. 1970. The seagrasses of the world. North Holland Publishing Co., Amsterdam.

den Hartog, C. 1994. Suffocation of a littoral *Zostera* bed by *Enteromorpha radiata*. Aquatic Botany **47**:21-28.

Donadi, S., van der Heide, T., Piersma, T., van der Zee, E. M., Weerman, E. J., van de Koppel, J., Olff, H., Devine, C., Hernawan, U. E., Boers, M., Planthof, L., and Klemens Eriksson, B. 2015. Multi-

scale habitat modification by coexisting ecosystem engineers drives spatial separation of macrobenthic functional groups. Oikos **124**:1502-1510.

Duarte, C. M., Fourqurean, J. W., Krause-Jensen, D., and Olesen, B. 2006. Dynamics of seagrass stability and change. Pages 271-294 *in* A. W. D. Larkum, R. J. Orth, and C. M. Duarte, editors. Seagrasses: Biology, Ecology, and Conservation. Springer Netherlands, Dordrecht.

Duke, C. S., Litaker, W., and Ramus, J. 1989. Effects of temperature, nitrogen supply, and tissue nitrogen on ammonium uptake rates of the chlorophyte seaweeds *Ulva curvata* and *Codium decorticatum* Journal of Phycology **25**:113-120.

Ellison, A. M., Bank, M. S., Clinton, B. D., Colburn, E. A., Elliott, K., Ford, C. R., Foster, D. R., Kloeppel, B. D., Knoepp, J. D., and Lovett, G. M. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment **3**:479-486.

Everett, R. A. 1991. Intertidal distribution of infauna in a central California lagoon: The role of seasonal blooms of macroalgae. Journal of Experimental Marine Biology and Ecology **150**:223-247.

Fonseca, M. S., and Cahalan, J. A. 1992. A preliminary evaluation of wave attenuation by four species of seagrass. Estuarine, Coastal and Shelf Science **35**:565-576.

Fonseca, M. S., Fisher, J. S., Zieman, J. C., and Thayer, G. W. 1982. Influence of the seagrass, *Zostera marina* l., on current flow. Estuarine, Coastal and Shelf Science **15**:351-364.

Fry, B., Rogers, K., Barry, B., Barr, N., and Dudley, B. 2011. Eutrophication indicators in the Hutt River Estuary, New Zealand. New Zealand Journal of Marine and Freshwater Research **45**:665-677.

Gagnon, K., McKindsey, C. W., and Johnson, L. E. 2015. Roles of dispersal mode, recipient environment and disturbance in the secondary spread of the invasive seaweed *Codium fragile*. Biological Invasions **17**:1123-1136.

Geertz-Hansen, O., Sand-Jensen, K., Hansen, D. F., and Christiansen, A. 1993. Growth and grazing control of abundance of the marine macroalga, *Ulva lactuca* l. In a eutrophic Danish estuary. Aquatic Botany **46**:101-109.

Giannotti, A. L., and McGlathery, K. J. 2001. Consumption of *Ulva lactuca* (Chlorophyta) by the omnivorous mud snail *Ilyanassa obsoleta* (Say). Journal of Phycology **37**:209-215.

Grange, K. R. 1979. Soft-bottom macrobenthic communities of Manukau Harbour, New Zealand. New Zealand Journal of Marine and Freshwater Research **13**:315-329.

Green, E. P., and Short, F. T. 2003. World atlas of seagrasses. University of California Press, Berkeley, USA.

Gribben, P. E., and Wright, J. T. 2006. Invasive seaweed enhances recruitment of a native bivalve: roles of refuge from predation and the habitat choice of recruits. Marine Ecology Progress Series **318**:177-185.

Grizzle, R. E., Short, F. T., Newell, C. R., Hoven, H., and Kindblom, L. 1996. Hydrodynamically induced synchronous waving of seagrasses:'monami'and its possible effects on larval mussel settlement. Journal of Experimental Marine Biology and Ecology **206**:165-177.

Hall, L. M., Hanisak, M. D., and Virnstein, R. W. 2006. Fragments of the seagrasses *Halodule wrightii* and *Halophila johnsonii* as potential recruits in Indian River Lagoon, Florida. Marine Ecology Progress Series **310**:109-117.

Halun, Z., Terrados, J., Borum, J., Kamp-Nielsen, L., Duarte, C. M., and Fortes, M. D. 2002. Experimental evaluation of the effects of siltation-derived changes in sediment conditions on the Philippine seagrass *Cymodocea rotundata*. Journal of Experimental Marine Biology and Ecology **279**:73-87.

Han, Q. Y., and Liu, D. Y. 2014. Macroalgae blooms and their effects on seagrass ecosystems. Journal of Ocean University of China **13**:791-798.

Hanke, M. H., Posey, M. H., and Alphin, T. D. 2017. The effects of intertidal oyster reef habitat characteristics on faunal utilization. Marine Ecology Progress Series **581**:57-70.

Harwell, M. C., and Orth, R. J. 2002. Long-distance dispersal potential in a marine macrophyte. Ecology **83**:3319-3330.

Hauxwell, J., Cebrián, J., Furlong, C., and Valiela, I. 2001. Macroalgal canopies contribute to eelgrass (*Zostera marina*) decline in temperate estuarine ecosystems. Ecology **82**:1007-1022.

Hauxwell, J., McClelland, J., Behr, P. J., and Valiela, I. 1998. Relative importance of grazing and nutrient controls of macroalgal biomass in three temperate shallow estuaries. Estuaries **21**:347-360.

Heck , K. L., Carruthers, T. J. B., Duarte, C. M., Hughes, A. R., Kendrick, G., Orth, R. J., and Williams, S. W. 2008. Trophic transfers from seagrass meadows subsidize diverse marine and terrestrial consumers. Ecosystems **11**:1198-1210.

Heck, K. L., and Orth, R. J. 1980. Seagrass habitats: The roles of habitat complexity, competition and predation in structuring associated fish and motile invertebrate assemblages. Pages 449-464 *in* V. S. Kennedy, editor. Estuarine perspectives. Academic Press.

Heesch, S., Broom, J. E., Neill, K. F., Farr, T. J., Dalen, J. L., and Nelson, W. A. 2009. *Ulva*, *Umbraulva* and *Gemina*: Genetic survey of New Zealand taxa reveals diversity and introduced species. European Journal of Phycology **44**:143-154.

Helmuth, B., Veit, R., and Holberton, R. 1994. Long-distance dispersal of a subantarctic brooding bivalve (*Gaimardia trapesina*) by kelp-rafting. Marine Biology **120**:421-426.

Hendriks, I. E., Cabanellas-Reboredo, M., Bouma, T. J., Deudero, S., and Duarte, C. M. 2011. Seagrass meadows modify drag forces on the shell of the fan mussel *Pinna nobilis*. Estuaries and Coasts **34**:60-67.

Henriques, P. R. 1980. Faunal community structure of eight soft shore, intertidal habitats in the Manukau Harbour. New Zealand Journal of Ecology **3**:97-103.

Hernández, I., Peralta, G., Pérez-Lloréns, J. L., Vergara, J. J., and Niell, F. X. 1997. Biomass and dynamics of growth of *Ulva* species in Palmones River Estuary. Journal of Phycology **33**:764-772.

Höffle, H., Wernberg, T., Thomsen, M. S., and Holmer, M. 2012. Drift algae, an invasive snail and elevated temperature reduce ecological performance of a warm-temperate seagrass, through additive effects. Marine Ecology Progress Series **450**:67-80.

Hollever, J., and Bolton-Ritchie, L. 2016. Broad scale mapping of the estuary of the Heathcote and Avon rivers/Ihutai. Environment Canterbury.

Holmer, M., and Nielsen, R. M. 2007. Effects of filamentous algal mats on sulfide invasion in eelgrass (*Zostera marina*). Journal of Experimental Marine Biology and Ecology **353**:245-252.

Holmer, M., Wirachwong, P., and Thomsen, M. S. 2011. Negative effects of stress-resistant drift algae and high temperature on a small ephemeral seagrass species. Marine Biology **158**:297-309.

Holmquist, J. 1994. Benthic macroalgae as a dispersal mechanism for fauna: Influence of a marine tumbleweed. Journal of Experimental Marine Biology and Ecology **180**:235-251.

Holmquist, J. G. 1997. Disturbance and gap formation in a marine benthic mosaic: influence of shifting macroalgal patches on seagrass structure and mobile invertebrates. Marine Ecology Progress Series **158**:121-130.

Huntington, B. E., and Boyer, K. E. 2008. Effects of red macroalgal (*Gracilariopsis* sp.) abundance on eelgrass *Zostera marina* in Tomales Bay, California, USA. Marine Ecology Progress Series **367**:133-142.

Hyslop, B. T., and Davies, M. S. 1998. Evidence for abrasion and enhanced growth of *Ulva lactuca* L. In the presence of colliery waste particles. Environmental Pollution **101**:117-121.

Inglis, G. 2003. Seagrasses of new zealand. Pages 134-143 *in* E. P. Green and F. T. Short, editors. World atlas of seagrasses: Present status and future conservation. University of California Press, Berkeley, California.

Ingólfsson, A. 1995. Floating clumps of seaweed around Iceland: Natural microcosms and a means of dispersal for shore fauna. Marine Biology **122**:13-21.

Irlandi, E., Orlando, B., and Biber, P. 2004. Drift algae-epiphyte-seagrass interactions in a subtropical *Thalassia testudinum* meadow. Marine Ecology Progress Series **279**:81-91.
Irlandi, E. A. 1997. Seagrass patch size and survivorship of an infaunal bivalve. Oikos **78**:511-518.
Jones, M., and Pinn, E. 2006. The impact of a macroalgal mat on benthic biodiversity in Poole Harbour. Marine pollution bulletin **53**:63-71.
Jones, M. B., Marsden, I. D., and Holdaway, R. N. 2005. Life in the estuary: Illustrated guide and ecology. Canterbury University Press.
Josselyn, M. N., Cailliet, G. M., Niesen, T. M., Cowen, R., Hurley, A. C., Connor, J., and Hawes, S. 1983. Composition, export and faunal utilization of drift vegetation in the salt river submarine canyon. Estuarine, Coastal and Shelf Science **17**:447-465.
Jupp, K., Partridge, T., Hart, D., and Marsden, I. 2007. Ecology of the Avon-Heathcote Estuary: Comparative salt marsh survey 2006-2007. Estuarine research report 34. University of Canterbury. School of Biological Sciences.
Kidwell, S. M., and Jablonski, D. 1983. Taphonomic feedback: ecological consequences of shell accumulation. Pages 195-248 *in* M. J. S. Tevesz and P. L. McCall, editors. Biotic interactions in recent and fossil benthic communities. Springer US, Boston, MA.
Kilar, J. A., and Norris, J. N. 1988. Composition, export, and import of drift vegetation on a tropical, plant-dominated, fringing-reef platform (Caribbean Panama). Coral Reefs **7**:93-103.
Kopecky, A. L., and Dunton, K. H. 2006. Variability in drift macroalgal abundance in relation to biotic and abiotic factors in two seagrass dominated estuaries in the western Gulf of Mexico. Estuaries and Coasts **29**:617-629.
Kulczycki, G. R., Virnstein, R. W., and Nelson, W. G. 1981. The relationship between fish abundance and algal biomass in a seagrass-drift algae community. Estuarine, Coastal and Shelf Science **12**:341-347.
Lapointe, B. E., and Tenore, K. R. 1981. Experimental outdoor studies with *Ulva fasciata* delile. L. Interaction of light and nitrogen on nutrient uptake, growth, and biochemical composition. Journal of Experimental Marine Biology and Ecology **53**:135-152.
Lavery, P. S., Lukatelich, R. J., and McComb, A. J. 1991. Changes in the biomass and species composition of macroalgae in a eutrophic estuary. Estuarine, Coastal and Shelf Science **33**:1-22.
Liu, J., Wang, Z., and Lin, W. 2010. De-eutrophication of effluent wastewater from fish aquaculture by using marine green alga *Ulva pertusa*. Chinese Journal of Oceanology and Limnology **28**:201-208.
Logan, S. J. 1976. Ecology of *Diloma novaezelandiae* at Portobello, New Zealand. New Zealand Journal of Marine and Freshwater Research **10**:699-714.
Lubchenco, J. 1980. Algal zonation in the New England rocky intertidal community: An experimental analysis. Ecology **61**:333-344.
Lyons, D. A., Arvanitidis, C., Blight, A. J., Chatzinikolaou, E., Guy-Haim, T., Kotta, J., Orav-Kotta, H., Queirós, A. M., Rilov, G., and Somerfield, P. J. 2014. Macroalgal blooms alter community structure and primary productivity in marine ecosystems. Global Change Biology **20**:2712-2724.
Macias-Fauria, M., and Johnson, E. A. 2013. Warming-induced upslope advance of subalpine forest is severely limited by geomorphic processes. Proceedings of the National Academy of Sciences **110**:8117-8122.
Marsden, I. D., and Knox, G. A. 2008. Estuaries, harbours and inlets. Pages 735-770 *in* M. J. Winterbourn, editor. Natural history of canterbury. University of Canterbury Press, Christchurch, New Zealand.
Marshall, B. A. 1998. The new zealand recent species of *cantharidus* montfort, 1810 and *micrelenchus* finlay, 1926 (mollusca: Gastropoda: Trochidae). Molluscan Research **19**:107-156.

McGlathery, K. J. 2001. Macroalgal blooms contribute to the decline of seagrass in nutrient-enriched waters. Journal of Phycology **37**:453-456.

McQuaid, C. D. 1982. The influence of desiccation and predation on vertical size gradients in populations of the gastropod *Oxystele variegata* (Anton) on an exposed rocky shore. Oecologia **53**:123-127.

Micheli, F., and Peterson, C. H. 1999. Estuarine vegetated habitats as corridors for predator movements. Conservation Biology **13**:869-881.

Mills, V. S., and Berkenbusch, K. 2009. Seagrass (*Zostera muelleri*) patch size and spatial location influence infaunal macroinvertebrate assemblages. Estuarine, Coastal and Shelf Science **81**:123-129.

Molina-Montenegro, M. A., Muñoz, A. A., Badano, E. I., Morales, B. W., Fuentes, K. M., and Cavieres, L. A. 2005. Positive associations between macroalgal species in a rocky intertidal zone and their effects on the physiological performance of *Ulva lactuca*. Marine Ecology Progress Series **292**:173-180.

Morris, D. W. 1990. Temporal variation, habitat selection and community structure. Oikos **59**:303-312.

Mvungi, E. F., Lyimo, T. J., and Björk, M. 2012. When *Zostera marina* is intermixed with *Ulva*, its photosynthesis is reduced by increased pH and lower light, but not by changes in light quality. Aquatic Botany **102**:44-49.

Newell, R. I., and Koch, E. W. 2004. Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. Estuaries **27**:793-806.

Norkko, J., Bonsdorff, E., and Norkko, A. 2000. Drifting algal mats as an alternative habitat for benthic invertebrates: Species specific responses to a transient resource. Journal of Experimental Marine Biology and Ecology **248**:79-104.

Paine, R. T., and Vadas, R. L. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. Limnology and Oceanography **14**:710-719.

Peterson, B. J., and Heck Jr, K. L. 2001. Positive interactions between suspension-feeding bivalves and seagrass-a facultative mutualism. Marine Ecology Progress Series **213**:143-155.

Pickering, T. D., Gordon, M. E., and Tong, L. J. 1990. Seasonal growth, density, reproductive phenology and agar quality of *Gracilaria sordida* (Gracilariales, Rhodophyta) at Mokomoko Inlet, New Zealand. Hydrobiologia **204**:253-262.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raffaelli, D. G., Raven, J. A., and Poole, L. J. 1998. Ecological impact of green macroalgal blooms. Oceanography and Marine Biology: an annual review **36**:97-125.

Reise, K. 2002. Sediment mediated species interactions in coastal waters. Journal of Sea Research **48**:127-141.

Reusch, T. B. H. 1998. Differing effects of eelgrass *Zostera marina* on recruitment and growth of associated blue mussels *Mytilus edulis*. Marine Ecology Progress Series **167**:149-153.

Rochefort, R. M., Little, R. L., Woodward, A., and Peterson, D. L. 1994. Changes in sub-alpine tree distribution in western North America: A review of climatic and other causal factors. The Holocene **4**:89-100.

Rooney, T. P. 2001. Deer impacts on forest ecosystems: A North American perspective. Forestry: An International Journal of Forest Research **74**:201-208.

Sanmartí, N., Solé, L., Romero, J., and Pérez, M. 2018. Seagrass-bivalve facilitative interactions: trait-mediated effects along an environmental gradient. Marine Environmental Research **133**:99-104.

Schiel, D. R. 2011. Biogeographic patterns and long-term changes on New Zealand coastal reefs: non-trophic cascades from diffuse and local impacts. Journal of Experimental Marine Biology and Ecology **400**:33-51.

Schiel, D. R., and Lilley, S. A. 2007. Gradients of disturbance to an algal canopy and the modification of an intertidal community. Marine Ecology Progress Series **339**:1-11.

Schiel, D. R., and Lilley, S. A. 2011. Impacts and negative feedbacks in community recovery over eight years following removal of habitat-forming macroalgae. Journal of Experimental Marine Biology and Ecology **407**:108-115.

Schiel, D. R., and Nelson, W. A. 1990. The harvesting of macroalgae in New Zealand. Hydrobiologia **204**:25-33.

Sfriso, A., Wolf, M. A., Maistro, S., Sciuto, K., and Moro, I. 2012. Spreading and autoecology of the invasive species *Gracilaria vermiculophylla* (Gracilariales, Rhodophyta) in the lagoons of the north-western Adriatic Sea (Mediterranean Sea, Italy). Estuarine, Coastal and Shelf Science **114**:192-198.

Shank, T. M., Fornari, D. J., Von Damm, K. L., Lilley, M. D., Haymon, R. M., and Lutz, R. A. 1998. Temporal and spatial patterns of biological community development at nascent deep-sea hydrothermal vents (9°50'N, East Pacific Rise). Deep Sea Research Part II: Topical Studies in Oceanography **45**:465-515.

Short, F., Carruthers, T., Dennison, W., and Waycott, M. 2007. Global seagrass distribution and diversity: a bioregional model. Journal of Experimental Marine Biology and Ecology **350**:3-20.

Short, F. T., and Wyllie-Echeverria, S. 1996. Natural and human-induced disturbance of seagrasses. Environmental Conservation **23**:17-27.

Shpigel, M., Neori, A., Popper, D. M., and Gordin, H. 1993. A proposed model for "environmentally clean" land-based culture of fish, bivalves and seaweeds. Aquaculture **117**:115-128.

Sousa, R., Gutiérrez, J., and Aldridge, D. 2009. Non-indigenous invasive bivalves as ecosystem engineers. Biological Invasions **11**:2367-2385.

Taylor, R. B. 1997. Seasonal variation in assemblages of mobile epifauna inhabiting three subtidal brown seaweeds in northeastern New Zealand. Hydrobiologia **361**:25-35.

Thomsen, M., Stæhr, P., Nejrup, L., and Schiel, D. 2013. Effects of the invasive macroalgae *Gracilaria vermiculophylla* on two co-occurring foundation species and associated invertebrates. Aquatic Invasions **8**:133-145.

Thomsen, M. S. 2004. Species, thallus size and substrate determine macroalgal break force and break location in a low-energy soft-bottom lagoon. Aquatic Botany **80**:153-161.

Thomsen, M. S. 2010. Experimental evidence for positive effects of invasive seaweed on native invertebrates via habitat-formation in a seagrass bed. Aquatic Invasions **5**:341-346.

Thomsen, M. S., Alestra, T., Brockerhoff, D., Lilley, S. A., South, P. M., and Schiel, D. R. 2018. Modified kelp seasonality and invertebrate diversity where an invasive kelp co-occurs with native mussels. Marine Biology **165**:173.

Thomsen, M. S., Hildebrand, T., South, P. M., Foster, T., Siciliano, A., Oldach, E., and Schiel, D. R. 2016. A sixth-level habitat cascade increases biodiversity in an intertidal estuary. Ecology and evolution **6**:8291-8303.

Thomsen, M. S., and McGlathery, K. J. 2007. Stress tolerance of the invasive macroalgae *Codium fragile* and *Gracilaria vermiculophylla* in a soft-bottom turbid lagoon. Biological Invasions **9**:499-513.

Thomsen, M. S., Staehr, P. A., Nyberg, C. D., Schwærter, S., Krause-Jensen, D., and Silliman, B. R. 2007. *Gracilaria vermiculophylla* (ohmi) Papenfuss, 1967 (Rhodophyta, Gracilariaceae) in northern Europe, with emphasis on Danish conditions, and what to expect in the future. Aquatic Invasions.

Turner, S., and Schwarz, A.-M. 2006. Management and conservation of seagrass in New Zealand: an introduction. Science for Conservation 264:1-90.

Turner, S. J., Hewitt, J. E., Wilkinson, M. R., Morrisey, D. J., Thrush, S. F., Cummings, V. J., and Funnell, G. 1999. Seagrass patches and landscapes: the influence of wind-wave dynamics and hierarchical arrangements of spatial structure on macrofaunal seagrass communities. Estuaries **22**:1016-1032.

Valentine, J. R., and Heck, K. 1993. Mussels in seagrass meadows: their influence on macroinvertebrate abundance and secondary production in the northern Gulf of Mexico. Marine Ecology Progress Series **96**:63-74.

Valiela, I., McClelland, J., Hauxwell, J., Behr, P. J., Hersh, D., and Foreman, K. 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnology and Oceanography **42**:1105-1118.

Valiente-Banuet, A., and Ezcurra, E. 1991. Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacan Valley, Mexico. Journal of Ecology **79**:961-971.

van der Heide, T., van Nes, E. H., Geerling, G. W., Smolders, A. J. P., Bouma, T. J., and van Katwijk, M. M. 2007. Positive feedbacks in seagrass ecosystems: implications for success in conservation and restoration. Ecosystems **10**:1311-1322.

Vanderklift, M. A., and Wernberg, T. 2008. Detached kelps from distant sources are a food subsidy for sea urchins. Oecologia **157**:327-335.

Virnstein, R. W., and Carbonara, P. A. 1985. Seasonal abundance and distribution of drift algae and seagrasses in the mid-Indian River Lagoon, Florida. Aquatic Botany **23**:67-82.

Wagner, E., Dumbauld, B. R., Hacker, S. D., Trimble, A. C., Wisehart, L. M., and Ruesink, J. L. 2012. Density-dependent effects of an introduced oyster, *Crassostrea gigas*, on a native intertidal seagrass, *Zostera marina*. Marine Ecology Progress Series **468**:149-160.

Wall, C. C., Peterson, B. J., and Gobler, C. J. 2008. Facilitation of seagrass *Zostera marina* productivity by suspension-feeding bivalves. Marine Ecology Progress Series **357**:165-174.

Wernberg, T., Tuya, F., Thomsen, M. S., and Kendrick, G. 2010. Turban snails as habitat for foliose algae: contrasting geographical patterns in species richness. Marine and Freshwater Research **61**:1237-1242.

Wernberg, T., Vanderklift, M. A., How, J., and Lavery, P. S. 2006. Export of detached macroalgae from reefs to adjacent seagrass beds. Oecologia **147**:692-701.

Wolff, T. 1976. Utilization of seagrass in the deep sea. Aquatic Botany **2**:161-174.

Wright, J. T., Byers, J. E., DeVore, J. L., and Sotka, E. E. 2014. Engineering or food? Mechanisms of facilitation by a habitat-forming invasive seaweed. Ecology **95**:2699-2706.

Yarrington, C. S., Tyler, A. C., and Altieri, A. H. 2013. Do snails facilitate bloom-forming macroalgae in a eutrophic estuary? Journal of Experimental Marine Biology and Ecology **446**:253-261.

Zertuche-González, J. A., Camacho-Ibar, V. F., Pacheco-Ruíz, I., Cabello-Pasini, A., Galindo-Bect, L. A., Guzmán-Calderón, J. M., Macias-Carranza, V., and Espinoza-Avalos, J. 2009. The role of *Ulva* spp. as a temporary nutrient sink in a coastal lagoon with oyster cultivation and upwelling influence. Journal of Applied Phycology **21**:729.

Zhang, J., Kim, J. K., Yarish, C., and He, P. 2016. The expansion of *Ulva prolifera* O.F. Müller macroalgal blooms in the Yellow Sea, PR China, through asexual reproduction. Marine pollution bulletin **104**:101-106.

Zimmerman, R., Gibson, R., and Harrington, J. 1979. Herbivory and detritivory among gammaridean amphipods from a Florida seagrass community. Marine Biology **54**:41-47.

Supplementary Material

Figure S1A. An example from experiment 2: seagrass removal plot (ca. 40 cm diameter) without mussels or *Ulva*.

Figure S1B. An example from experiment 2: Undisturbed seagrass control (ca. 40 cm diameter) with 4 mussels and 150 mL *Ulva*.

Figure S1C. An example from experiment 2: Seagrass removal plot (ca. 40 cm diameter) with 4 mussels and 500 mL *Ulva*.

CHAPTER 4 BIOGENIC HABITAT ASSOCIATIONS IN ESTUARIES: ASSESSMENT OF HABITAT-USERS AND HABITAT-FORMERS IN NEW ZEALAND

Abstract

Foundation species are ecologically important organisms that facilitate biological communities by modifying and creating biogenic habitats, for example, by providing a physical structure for other species to inhabit. In sedimentary estuaries, hard biogenic substrate, like shells, can be a limiting factor for many organisms. Estuarine communities are often analysed in a context of trophic interactions embedded in food-webs, but the same communities have not been analysed in a context of physical habitat associations. I therefore quantified all biogenic habitat associations in quadrats collected from 14 estuaries across three latitudinal regions (quadrat size = 0.01 m^2), and in more detail in the Avon-Heathcote Estuary (quadrat size = 0.0625 m^2) on the South Island of New Zealand. All surface-dwelling organisms were identified, counted, and classified as either habitat-formers or habitat-users, and all habitat-attachment interactions recorded (e.g., as 'habitat-using limpet attached to habitat-forming dead shell'). The latitudinal survey showed that (1) the southern estuaries had lowest richness of habitat-formers (2.4 ± 0.2 $quadrat^{-1}$), habitat-users (3.7 ± 0.3 $quadrat^{-1}$), and fewest habitat interactions (26.1 ± 4.6 $quadrat^{-1}$), (2) northern regions had the highest richness of habitat-formers (3.4 ± 0.2 $quadrat^{-1}$) and habitat-users (5.4 ± 0.3 $quadrat^{-1}$), and (3) central estuaries had highest number of habitat interactions (57.9 ± 14.4 $quadrat^{-1}$). In the Avon-Heathcote, I found highest richness of habitat-formers at silty sites (6.2 ± 0.3 $quadrat^{-1}$), lowest richness at muddy sites (4.3 ± 0.6 $quadrat^{-1}$), whereas seagrass and sandy sites had highest and lowest richness of habitat-users, respectively (9.1 ± 0.6 vs. 6.9 ± 1.0 $quadrat^{-1}$; there were no differences in the number of interactions between sites). I also found that living bivalves, seagrass, seaweeds, as well as species often overlooked as foundation species, such as dead bivalve shells, snails, and encrusting bryozoans, were important habitat formers across estuaries and sites in New Zealand. These results highlight the importance of biogenic habitat interactions in intertidal sedimentary estuaries, suggesting that these interactions may also be important in other systems where hard substrates are limited, and desiccation stress is high.

Introduction

An organism's use of 'habitat' has been an important concept since Aristotle's works in *History of Animals* written in 350 BCE (Aristotle, trans. 1910). Over time, the definition of habitat has changed, which has led to misinterpretations and confusion (see Hall et al. 1997, Rountree and Able 2007 for reviews). Here I apply the 'organismal habitat' definition in which a habitat is "the resources and conditions present in an area that produce occupancy by a given individual organism, population, species or community" (Rountree and Able 2007). Some organisms provide physical habitat, along with many other ecosystem functions, and are known as foundation species (Dayton 1972, Ellison et al. 2005) (also referred to as structural species (Huston 1994) or physical ecosystem engineers (Jones et al. 1997)). For example, in forests there are many interacting organisms that depend on 'primary' habitat-forming trees (Ellison et al. 2005, Mayfield et al. 2005, Nadrowski et al. 2010) and nested within this forest is a mosaic of smaller-scale habitats where organisms may only inhabit canopies, tree trunks, or the forest floor (Schoener 1974, Dickson and Noble 1978, Pacala and Roughgarden 1985, Koen 1988, Yanoviak and Kaspari 2003). Similar habitat mosaics exist in other ecosystems, including seagrass beds, savannahs, coral reefs, and sedimentary estuaries (Heck Jr and Orth 1980, Pringle et al. 1988, Snyder and Best 1988, Albrecht and Gotelli 2001, Stachowicz 2001).

In many ecosystems, foundation species interact within these mosaics of habitats, resulting in facilitation of organisms ('habitat-users') that depend on the formation of biogenic habitat ('habitat-formers') (Altieri et al. 2007, Thomsen et al. 2010a, Bishop et al. 2012, Watson and Herring 2012, Angelini and Silliman 2014, Thomsen and Wernberg 2014, Angelini et al. 2015). A few species interactions are particularly important in determining community and ecosystem structures, including trophic interactions (Price et al. 1980, Carpenter et al. 1985, Leibold 1989), parasitism (Barber et al. 2000, Mouritsen and Poulin 2006, Tylianakis et al. 2006), competition (Connell 1961, Tilman 1994) and mutualism (Ackerman 1983, Olesen and Jordano 2002, Stouffer et al. 2014) - processes that have been analysed in great detail in interaction webs (Olesen and Jordano 2002, Rybarczyk and Elkaïm 2003, Araújo et al. 2008). By contrast, few studies have analysed how community-wide biogenic habitat formation also modulate species-interactions, and these few studies have only analysed habitat-interactions between a small number of species within a limited area (see Angelini et al. 2015, Thomsen et al. 2016, Yakovis and Artemieva 2017).

Sedimentary estuaries are often described as ‘bare’ and ‘uniform’ mudflats (Ward et al. 2003, Cusson and Bourget 2005, Saint-Béat et al. 2014, Thomsen et al. 2019), but mosaics of biogenic habitats composed of seagrass, seaweed, bivalves, and snails can be common (Heck Jr and Orth 1980, Peterson 2003, McLeod et al. 2013, Donadi et al. 2015, Gain et al. 2016). Seagrasses, for example, are typical estuarine foundation species that stabilize sediments, slow water currents, buffer against waves, and provide physical habitat for many organisms (Fonseca and Cahalan 1992, Boström et al. 2006, Connolly and Hindell 2006, Orth et al. 2006, Herkül and Kotta 2009, Carr et al. 2010, Schmidt et al. 2011). Similarly, seaweeds, can also act as foundation species, although often are less stable across seasons and sites (Virnstein and Carbonara 1985, Airoldi 2000, Irlandi et al. 2004, Rasmussen et al. 2013, Ramus et al. 2017, Thomsen et al. 2019). Nevertheless, seaweeds provide complex physical habitat and can affect water and sediment chemistry, especially during bloom events (Raffaelli et al. 1998, Marsden and Bressington 2009, Mvungi et al. 2012, Thomsen and Wernberg 2015, Ramus et al. 2017). Finally, bivalves and snails can provide habitat through their calcium carbonate shells, and these shells function as ‘mini-islands’ of hard substrate in a sea of soft sediments that sometimes form larger reef structures (Suchanek 1992, Seed 1996, Wahl 1996, Ricciardi et al. 1997, Wernberg et al. 2010, Thyrring et al. 2013). When and where foundation species dominate in estuaries, facilitation and habitat cascades can also occur (Altieri et al. 2007, Thomsen et al. 2010a, Angelini et al. 2011). For example, intertidal cordgrass provides habitat for mussels, which in turn provide hard substrate habitat for different macroinvertebrates (Altieri et al. 2007, Angelini et al. 2015). Similarly, it has been shown that estuarine bivalves can provide habitat to seaweeds, which then provide habitat to snails that can provide habitat to bryozoans, which in turn, provide habitat to seaweeds (Thomsen et al. 2016).

The scale of habitat use is essential to understand community dynamics (Morris 1987) and research should therefore merge broad- and fine-scale data collections, as used for marine mammals (Ballance 1992, Allen et al. 2001), migrating birds (Colwell and Landrum 1993, Naugle et al. 1999), fish (Lamouroux et al. 1999, Furey et al. 2013), and snails (Genner and Michel 2003, Moreno-Rueda 2006). Still, most habitat interaction research has focused only on small subsets of a large interacting community, and broader examinations (such as geographic differences and between tidal elevations) would help to refine knowledge about the importance of habitat formation in controlling community structures. This chapter aims to enumerate and compare interactions between benthic habitat-formers and -users in estuaries

on the South Island of New Zealand for different latitudinal regions, tidal elevations, and habitat types. This objective was addressed through a broad-scale latitudinal survey of 14 estuaries in three regions of the South Island, and a more detailed survey at nine sites in the Avon-Heathcote Estuary in Christchurch. More specifically, I hypothesized that the number of habitat-formers, habitat-users and habitat-interactions were higher:

- in northern than southern estuaries, because northern estuaries are warmer, potentially following classic geographic patterns of decreasing species richness with increasing latitude.
- at low than high tidal elevation, because many organisms may be absent from high elevation habitats due to desiccation and temperature stress (Menge and Sutherland 1987, Harley and Helmuth 2003)
- associated with seagrass beds, because seagrasses are known to facilitate a wide variety of marine organisms (Heck and Orth 1980, Boström et al. 2006).
- in larger than smaller quadrats, following simple well established species-area relationships (MacArthur and Wilson 1967, Simberloff 1976).
- during night than day, because some mobile species may migrate to deeper waters or hide in the sediment during the day to avoid predators and abiotic stress (Underwood 1979, Jacobsen and Stabell 1999).

Methods

Study sites

To test for commonality and consistency of biogenic habitat interactions across latitudes and tidal elevations, a broad-scale survey was done in 14 estuaries with known seagrass beds around the South Island, New Zealand during low tide (Figure 4.1). Six estuaries from the northern region were sampled in April 2016: Puponga Inlet (40°31'35.0"S 172°44'07.0"E), Ruataniwha Inlet (40°39'18.3"S 172°40'31.7"E), Nelson Haven (41°13'51.4"S 173°18'33.4"E), Delaware Bay (41°10'05.6"S 173°26'33.6"E), Okiwa Bay (41°15'58.3"S 173°54'54.6"E), and Ngakuta Bay (41°16'22.5"S 173°57'47.9"E). Three were sampled from the central region in August 2016: Robinson's Bay (43°45'51.5"S 172°57'26.5"E), Duvauchelle Bay (43°45'11.3"S 172°55'45.0"E), and Avon-Heathcote Estuary (43°33'09.3"S 172°44'40.5"E). Finally, five estuaries were sampled from the southern region in October 2016: Portobello Bay (45°49'21.6"S 170°39'58.3"E), Papanui Inlet (45°50'32.7"S 170°41'33.0"E), Dowling Bay (45°47'18.8"S 170°39'45.7"E), Catlins River Estuary (46°28'46.9"S 169°41'26.4"E), and Jacobs River Estuary (46°20'42.1"S 168°01'04.3"E).

Additional, more detailed surveys were carried out in the Avon-Heathcote Estuary situated in Christchurch, New Zealand (43°33'09.3"S 172°44'40.5"E). The Avon-Heathcote Estuary is a ~8.8 km^2 shallow, well-flushed, bar-built estuary. Two rivers flow into the estuary, the Avon River flows from the north and the Heathcote River from the southwest (Figure 4.1). Seagrass beds are present on the eastern side of the estuary and cover about 0.35 km^2. Seaweed biomass varies over the year but can cover up to 1.4 km^2 whereas dead shell beds constitute ca. 0.5 km^2 of the estuary (Hollever and Bolton-Ritchie 2016).

Latitudinal survey

Background habitat cover and habitat use

Six 10 × 10 cm (0.010 m^2) quadrats were sampled haphazardly across benthic habitats in the intertidal-subtidal transition zone and six were collected from a higher elevation area (at least 10 m higher than the intertidal-subtidal transition zone) during low tide. A photo was taken of each quadrat, perpendicular to the substrate. Percent covers of key habitat-forming species (seagrass, seaweed, dead shell, rock) and bare sediment, were later quantified from these photos (analysed with a maximum cover of 100%, so that if a seaweed frond entirely covered a shell, only the seaweed was quantified). Unfortunately, quadrat photos from the southern estuaries were lost. However, percent coverage of habitat-forming organisms could still be analysed because similar photos from a different benthic substrate survey were taken from the same estuaries at the same time, (i.e., the southern estuaries background habitat-cover data are not in a one-to-one relationship with the habitat-use data, see below).

Each quadrat was subsequently inspected *in situ* for the presence of habitat-formers, habitat-users, and habitat-interactions. Habitat use was quantified as (a) mobile organisms observed on/in/under or (b) sessile organisms attached to another biogenic structure. For example, snails could be attached to the underside of drift seaweed and crabs could hide inside dead shells. The habitat use of every individual within the quadrat that was visible to the naked eye (≥ 0.5 mm) was determined. If an individual (such as an *Ulva* frond or a partially buried shell) was large or dirty, the habitat-formers were carefully rinsed in a 500 µm sieve with local seawater to record interactions with potential hidden habitat-users. Any mobile organism that fell into the sieve during the rinse was considered to be associated with the collected habitat-former (because every other visible habitat-use interaction had already been recorded). All 'binary' habitat-interactions between two organisms, such as 'snail-attached-

to-seaweed' or 'bryozoan-attached-to-snail', were recorded for all organisms above and within the first 1 cm of the sediment (searching for shallow buried biogenic material such as living bivalves or dead shells). This analysis, however, does not include deeper burrowing organisms, such as polychaetes or bivalves positioned below 1 cm depth. Encrusting and colonial organisms, such as bryozoans and the brown seaweed *Ralfsia* spp., were recorded only as being present or absent. An example is provided in the supplementary material to further describe this methodology.

Factorial analysis of variance (ANOVA) tested for effects of latitudinal region and tidal elevation (fixed factors) on the number of habitat interactions (converted to m^2 to enable comparisons between surveys and methods), richness of habitat-formers, and richness of habitat-users. Homogeneity of variances were checked with Levene's tests (package *'car'*). If the variance homogeneity assumption was violated, data were transformed (log 10 or square-root) and rechecked. If variances were still heterogeneous, alpha was reduced to 0.01. Alpha was 0.05 in all tests, unless otherwise noted. Tukey's Honest Significant Difference post hoc tests were used following significant ANOVA tests. Analyses were performed in R version 3.5.0 (R Core Team 2017).

Surveys in the Avon Heathcote Estuary

Background habitat cover and habitat use

Habitat interactions and taxa richness of habitat-formers and habitat-users were assessed in the Avon-Heathcote Estuary in December 2015 - May 2016 (Figure 4.1). Four sites were sampled along the eastern peninsula (the Spit), and five sites along the longer southern coastline (the Causeway). These nine sites represent four habitats: muddy and organic rich sediments near rivers, silty sediments, sandy sediments near the ocean, and seagrass beds (Figure 4.1). This local survey, when compared to the latitudinal survey, less constrained by field sampling time, and was therefore done with larger 25 × 25 cm (0.0625 m^2) quadrats. At each site, three quadrats were collected in the intertidal-subtidal transition zone and four were collected from a high-tide area. Habitat-cover (photographs of quadrats) and habitat-interactions (visual observations of quadrats) were quantified, as described in the latitudinal survey. Factorial ANOVA tested for effects of habitat type and tidal elevation on number of habitat interactions and richness of habitat-formers and habitat-users. Assumption tests and post hoc analyses were conducted as described in the latitudinal survey.

Habitat use of mobile organisms between day and night

Habitat interactions involving mobile organisms were compared between day and night, as diurnal mobility patterns may influence results and data interpretations. Eight small quadrats (0.010 m^2) were sampled during low tide in January 2018 in an intertidal seagrass bed near Plover Street in the Avon-Heathcote Estuary (see Figure 1) during the day and, again, in the same seagrass patch, one hour after sunset. Only mobile habitat-users, such as snails and crabs, were quantified in this survey, because sessile organisms cannot change their habitat usage (but sessile organisms were, of course, counted if a mobile species used them as habitat). A white-LED headlamp was used to illuminate the quadrats during night sampling. ANOVA tested for effects of time of sampling on number of habitat interactions, richness of habitat-formers, and richness of habitat-users. Assumption tests and post hoc analyses were conducted as described in the latitudinal survey.

Quadrat size comparison

Because different quadrat sizes were used in different surveys, a specific quadrat size comparison was done in May 2018. The comparison was done near Tern Street (Figure 1) in the low tidal zone in three habitats: bare (unvegetated) sediment, dead shell accumulations, and a seagrass bed. The number of interactions was quantified as described above in both the small (0.010 m^2) and large (0.0625 m^2) quadrats (n = 3 per habitat and quadrat size). Factorial ANOVA tested for effects of quadrat size and habitat type on number of habitat interactions and richness of habitat-formers and habitat-users. Assumption tests and post hoc analyses were conducted as described in the latitudinal survey. Finally, species accumulation curves were constructed for both habitat-former and habitat-user richness using 999 permutations in PRIMER 6+. These curves were qualitatively assessed.

Results

Latitudinal survey

Background habitat cover

The northern estuaries were dominated by sediments (39%), followed by seagrass and seaweed (ca. 20% each), dead shells (12%) and rocks (9%; usually 4 mm fine pebbles to 32 mm coarse pebbles) (Figure 4.2A, B). The central and southern estuaries had relatively similar background habitat cover, also being dominated by sediments (55 vs. 42%,

respectively), followed by seagrass (30 vs. 25%), seaweed (10 vs. 17%), dead shells (5 vs. 10%) and rocks (0 vs. 6%, Figure 4.2A, B).

Habitat use

There were significant effects of region and elevation (but no interaction) on both habitat-interactions and richness of both habitat-formers and habitat-users (Table 4.1, Figure 4.3). The most habitat-interactions occurred in central estuaries ($p = 0.030$, 927.1 ± 229.6 m^{-2}), followed by northern estuaries (782.7 ± 126.5 m^{-2}) and least interactions in the southern estuaries (416.8 ± 73.4 m^{-2}, Figure 4.3A). In addition, samples from low elevation had significantly more interactions ($p = 0.023$, 764.9 ± 100.4 m^{-2}) than high elevation samples (436.9 ± 84.7 m^{-2}, Figure 4.3A). For the northern region, *Austrovenus stutchburyi* was involved in most habitat-interactions (29%), more specifically being inhabited by 1470.4 (± 328.4) organisms m^{-2}. The seaweed *Gracilaria chilensis* (15%, 790.1 ± 393.3 m^{-2}) and dead bivalve shells (12%, 639.4 ± 143.9 m^{-2}, Figure 4.4A, B) were also involved in many habitat-interactions. In the central estuaries, *Austrovenus* was again involved in most interactions (46%, 2705.5 ± 1428.3 m^{-2}) followed by the pulmonate snail *Amphibola crenata* (19%, 1144.4 ± 322.5 m^{-2}), and the trochid snail *Micrelenchus huttonii* (11%, 630.5 ± 324.7 m^{-2}, Figure 4.4C, D). Finally, in the southern estuaries dead bivalve shells were involved in most interactions (24%, 635.0 ± 151.9 m^{-2}) followed by *Austrovenus* (15%, 383.3 ± 87.5 m^{-2}), and *Ulva* (14%, 363.3 ± 288.5 m^{-2}, Figure 4.4E, F).

Taxonomic richness of habitat-formers was highest in northern estuaries ($p = 0.001$, 3.4 ± 0.2 $quadrat^{-1}$), followed by central (2.8 ± 0.2 $quadrat^{-1}$) and southern (2.4 ± 0.2 $quadrat^{-1}$) estuaries (Table 1B, Figure 3B). The low tidal elevation had, again, significantly more habitat-forming taxa ($p = 0.018$, 3.2 ± 0.2 $quadrat^{-1}$) than the high tidal elevation (2.6 ± 0.2 $quadrat^{-1}$ Figure 3B). Finally, richness of habitat-users showed a similar pattern to habitat-formers, with greatest richness in northern estuaries ($p < 0.001$, 5.4 ± 0.3 $quadrat^{-1}$), followed by central (4.0 ± 0.4 $quadrat^{-1}$) and southern (3.7 ± 0.3 $quadrat^{-1}$) estuaries, and with significantly higher richness at low ($p < 0.001$, 5.2 ± 0.3 $quadrat^{-1}$) than high (3.7 ± 0.3 $quadrat^{-1}$) elevation (Table 1C, Figure 3C).

Surveys in the Avon-Heathcote Estuary

Background habitat cover

Background habitat cover was relatively similar between the muddy river sites and nearby silty sites, dominated by sediments (66 vs. 70%) followed by seaweeds (31 vs. 27%) and dead bivalve shells (3 vs. 5%, Figure 4.5A, B). By comparison, the sandy sites had more dead shells (27%) and less seaweed (4%), whereas the seagrass site, obviously, had more seagrass (38%) but also less seaweed (8%) and less bare sediment (53%, Figure 4.5A, B).

Habitat use

The number of habitat interactions was not affected by either habitat type or elevations ($p > 0.05$, Table 4.2A, Figure 4.6A). For the muddy river sites, live *Austrovenus* were involved in most interactions (56% of all interactions, 996.6 ± 378.0 m^{-2}), followed by the snail *Amphibola* (11%, 200.0 ± 82.4 m^{-2}), and the red seaweed *Gigartina* spp. (9%, 154.3 ± 104.5 m^{-2}, Figure 4.7A, B). Similarly, at the nearby silty sites, live *Austrovenus* was again involved in most interactions (26%, 721.5 ± 87.1 m^{-2}), followed closely by another trochid snail, *Diloma nigerrimum* (25%, 680.4 ± 115.2 m^{-2}), and dead bivalve shells (14%, 376.4± 82.6 m^{-2}, Figure 4.7C, D). By contrast, at the sandy sites, dead shells were involved in the most interactions (81%, 3585.2 ± 1328.8 m^{-2}) with much fewer interactions by live *Austrovenus* (8%, 343.4 ± 105.4 m^{-2}, Figure 4.7E, F). Finally, at the seagrass sites, *Zostera* was, not surprisingly, involved in most interactions (39%, 730.3 ± 164.9 m^{-2}) followed by *Micrelenchus* (25%, 458.3 ± 126.0 m^{-2}) and dead shells (14%, 259.4 ± 87.4 m^{-2}, Figure 4.7G, H). By contrast, richness of both habitat-formers and habitat-users were significantly affected by both habitat type and elevation (but with no significant interactions, Table 4.2B, C). More specifically, richness of habitat-forming organisms was highest at silty sites ($p = 0.013$, 6.2 ± 0.3 $quadrat^{-1}$), followed by seagrass sites (5.6 ± 0.2 $quadrat^{-1}$), sandy sites (4.8 ± 0.6 $quadrat^{-1}$), and finally muddy river sites (4.3 ± 0.6 $quadrat^{-1}$, Figure 4.6B). Furthermore, richness of habitat-formers was significantly higher at low than high tidal elevation ($p = 0.043$, 5.9 ± 0.3 vs. 4.9 ± 0.3 $quadrat^{-1}$, Figure 6B). For habitat-users, seagrass sites had the highest richness ($p = 0.032$, 9.1 ± 0.6 $quadrat^{-1}$), followed by silty sites (8.9 ± 0.5 $quadrat^{-1}$), muddy river sites (7.0 ± 1.0 $quadrat^{-1}$) and sandy sites (6.9 ± 1.0 $quadrat^{-1}$), and richness was, again, higher at low than the high elevations ($p = 0.028$, 9.3 ± 0.6 vs. 7.1 ± 0.5 $quadrat^{-1}$, Figure 4.6C).

Habitat use of mobile organisms between day and night

The analyses of mobile organisms in day versus night samples showed no differences in either the number of habitat interactions ($p = 0.484$, Table 4.3A, Figure 4.8A), richness of mobile habitat-formers ($p = 0.253$, Table 4.3B, Figure 4.8B), or richness of mobile habitat-users ($p = 0.837$, Table 4.3C, Figure 4.8C).

Quadrat size comparison

There was a significant interaction between quadrat size and habitat type ($p = 0.020$), but no single factor effects (p-Size = 0.401; p-Habitat = 0.749) for habitat-interactions (Table 4.4A, Figure 4.9A). However, post-hoc analysis did not find any significant pairwise differences (the lowest value, $p = 0.075$, was between the 0.0625 m^2 and 0.010 m^2 quadrats in the seagrass habitat). By contrast, richness of habitat-formers was significantly affected by both quadrat size ($p = 0.002$) and habitat ($p = 0.015$) but the interaction was not significant ($p = 0.686$, Table 4.4B, Figure 4.9B). More specifically, richness of habitat-formers was higher in the large than the small quadrats (4.9 ± 0.4 vs. 3.0 ± 0.4 quadrat^{-1}) and in seagrass beds (5.0 ± 0.5 quadrat^{-1}), followed by bare sediment (3.8 ± 0.6), and dead shells (3.0 ± 0.6, Table 4.4B, Figure 4.9B). However, the species-area curve was steeper for the small than the large quadrat, suggesting that small quadrats were more efficient to quantify richness of habitat-formers (Figure 4.9C). In addition, there were significant single factor effects, and a significant interaction, between habitat and size, on richness of habitat-users ($p = 0.001$, Table 4.4C). More species were, again, found in the large (7.7 ± 0.9 quadrat^{-1}) than in the small quadrats (5.0 ± 0.3 quadrat^{-1}) and in the shell (12.0 ± 1.2 quadrat^{-1}) and seagrass habitats (8.7 ± 0.9 quadrat^{-1}), compared to bare sediments (4.3 ± 0.3 quadrat^{-1}, Figure 4.9D). Finally, the species-area curve was, again, steeper for smaller than larger quadrats, highlighting that smaller quadrats were more efficient to quantify richness of habitat-users (Figure 4.9E)**.**

Discussion

Most studies about estuarine foundation species emphasize that seagrass and seaweed are important habitat-formers (Orth et al. 1984, Boström et al. 2006, Brun et al. 2009, Wright et al. 2010, Battley et al. 2011, Schmidt et al. 2011). Here, I show that many organisms not commonly considered foundation species, like dead shells, snails, and bryozoans, also

provide important habitat in sedimentary estuaries. In concert, these organisms create mosaics of habitats, providing layered structures of different complexities, shapes, textures, motilities, and sizes, and ultimately add niches to support diverse communities (Dayton 1972, Pringle et al. 1988, Stachowicz 2001, Ellison et al. 2005, Thomsen et al. 2016). In sedimentary systems such as estuaries, there are different types of biogenic hard substrata that add complexity and modify microclimates compared to an otherwise relatively homogenous 'bare' landscape (Ward et al. 2003, Cusson and Bourget 2005, Saint-Béat et al. 2014, Thomsen et al. 2019). My study also demonstrated that estuarine flora and fauna can inhabit many types of surfaces, including seaweeds, seagrass, living bivalves, dead bivalve shells, snails and bryozoans (Figure 4.4 and 4.7), potentially resulting in complex networks of facilitation and habitat cascades (Jones 1976, Atilla et al. 2003, Beekey et al. 2004, Ruiz et al. 2009, Thomsen et al. 2010a, Angelini et al. 2011, Altieri and Witman 2014, Thomsen and Wernberg 2014, Thomsen et al. 2016).

Latitudinal and elevation patterns

As hypothesized, I generally found higher richness of habitat-formers and habitat-users in northern estuaries and lowest richness in southern estuaries. This pattern might be caused by latitudinal gradients in environmental conditions. For example, across the sampled 6° difference in latitude, northern estuaries receive ca. 2400 hours of sun·year^{-1} and have an annual mean temperature of 13.8°C compared to only 1600 hours/y and annual mean temperature of 10.9°C in the southern region (Macara 2016, NIWA 2016). These results support other studies that have shown lower diversity of estuarine taxa at colder high latitudes (Duke et al. 1998, Engle and Summers 1999, Attrill et al. 2001). Species richness in New Zealand also tends to follow this latitudinal pattern for other organismal groups, as documented for snails (Barker 2005, Overton et al. 2009), fish (McClatchie et al. 1997, Francis et al. 2011) and trees (Bellingham et al. 1999, McGlone et al. 2010). Other co-varying factors may potentially partly explain observed patterns, such as biogeographical events and source-sink dynamics of larval dispersal (Banks et al. 2007, Chiswell and Rickard 2011, Sanford and Kelly 2011), coastal topography and geology, ocean current patterns, upwelling events, nutrient flows (Chiswell and Schiel 2001, Banks et al. 2007, Ross et al. 2009, Schiel 2011, Keeney et al. 2013), or idiosyncratic estuarine features such as catchment

area, or type or size of estuary (Smith and Duke 1987, Harris 2001, Hastie and Smith 2006, Asmala et al. 2013).

The number of habitat interactions and species richness of habitat-formers and habitat-users were, as hypothesized, higher at low than high tidal elevations (although this was not significant for the number of habitat interactions in the Avon-Heathcote survey). I expected more interactions at low elevations because short emergence times reduce physiological and environmental stress (Menge and Sutherland 1987, Peterson 1991, Harley and Helmuth 2003) with fewer restrictions on feeding and respiration (Underwood 1979, Little 1989, Peterson 1991).Still, some organisms, like barnacles, snails (e.g., *Diloma*, *Amphibola*, *Cominella*), and limpets (*Notoacmea* spp.) were involved in more interactions at high elevations across the latitudes, estuaries, and sites. Except for barnacles, these organisms are mobile species that can move to microhabitats where desiccation stress is mitigated, for example to scattered seaweed fronds (Wright et al. 2014) or wet sediments (Mitchell 1980). In addition, these organisms have adaptations to reduce desiccation stress, such as closing opercula or close-suction to substrates (Foster 1971, Shumway and Marsden 1982, Lowell 1984), and some taxa (e.g., *Amphibola, Diloma*) have high desiccation tolerances (Mitchell 1980, Shumway and Marsden 1982). These results highlight that biogenic structures provide important habitats in estuarine systems, and when species richness is low due to environmental stress.

Species and habitat types

Seagrasses are foundation species that create complex habitat and hotspots of biodiversity (Heck and Orth 1980, Orth et al. 1984, van Houte-Howes et al. 2004, Boström et al. 2006, Connolly and Hindell 2006, and Chapters 2 and 3). *Zostera muelleri,* the only seagrass species in New Zealand (Jacobs et al. 2006, Jones et al. 2008, Matheson et al. 2011), has short leaves (5-15 cm) compared to most seagrass species (Inglis 2003, Mills and Berkenbusch 2009) and is relatively common in the intertidal zone of sheltered estuaries where it forms mosaics of patches and larger beds (Inglis 2003). In New Zealand, *Zostera muelleri* is a habitat-former that can facilitate crabs (Woods and Schiel 1997, Alfaro 2006, Battley et al. 2011), bivalves (van Houte-Howes et al. 2004, Alfaro 2006), fish (Francis et al. 2005), and other benthic macroinvertebrates (Turner and Schwarz 2006, Mills and Berkenbusch 2009, Battley et al. 2011). However, my hypothesis that *Zostera* therefore should be the most important habitat-former involved in the most habitat-interactions across

all data was not supported, even though it was sampled in all estuaries (it was only among the 10 most important habitat-formers across all latitudes, sites, and elevations). My results showed instead that different, less studied taxa often were more important habitat for estuarine benthic communities in this study.

For example, seaweeds also provide biogenic habitat, such as the cosmopolitan green seaweed, *Ulva* spp., and red, branched *Gracilaria* spp. Worldwide, these seaweeds have positive effects on estuarine invertebrate communities through habitat formation, stress buffering, and as food sources. However, these seaweeds also form large decomposing mats with associated hypoxia and anoxia and smothering, thereby switching to negative effects on the same invertebrates (Wilson et al. 1990, Raffaelli et al. 1998, Thomsen et al. 2012a, Thomsen et al. 2013, Wernberg et al. 2013, Guidone et al. 2014, Queiroz and Dias 2014, Munari et al. 2015). My sampling consisted mostly of scattered patches of *Ulva* spp. and *Gracilaria chilensis* and results supported that seaweeds can have strong facilitative effects on a variety of organisms, particularly grazing snails, suggesting seaweeds can be a direct food source (see Chapter 6 for details – grazing). I also found that several other seaweeds species provided attachment space in individual estuaries, including the well-studied *Codium fragile* (Bulleri et al. 2006, Schmidt and Scheibling 2006, Drouin et al. 2011, Dijkstra et al. 2017), and less studied, *Gigartina* spp. (but see Dean and Connell 1987, Rosenfeld et al. 2015, Thomsen et al. 2016) and *Colpomenia bullosa*.

While seagrasses and seaweeds were important habitat-formers in both the latitudinal and local surveys, these aquatic plants had fewer interactions than shell-forming invertebrates like the endemic bivalve *Austrovenus*, dead shells of *Austrovenus*, and surface-dwelling mobile snails. These organisms were present in most samples collected across latitudes, tidal elevations, and sites. These shell-forming taxa, especially snails and dead bivalve shells, are often overlooked as habitat-formers (but see Dauer et al. 1982, Ricciardi et al. 1997, Gutiérrez et al. 2003, Summerhayes et al. 2009, Wernberg et al. 2010, Thomsen et al. 2016). *Austrovenus* is one of the most abundant shell-formers in New Zealand estuaries (Thrush et al. 2006, Williams et al. 2006, Sandwell et al. 2009, Kainamu-Murchie et al. 2018) and it has a short siphon causing its shell to protrude above the sediment surface. Live *Austrovenus* thereby provide hard substrates that are colonized by estuarine plants and animals (Whitlatch et al. 1997, Mouritsen and Poulin 2003, Thomsen et al. 2016). Furthermore, entire individuals can be found on the sediment surface, especially if they are heavily infected by parasites (Thomas et al. 1998, Thomas et al. 1999, Mouritsen 2002, Leung and Poulin 2007).

Austrovenus can occur in densities up to 4500 m^{-2} (Richardson et al. 1979, Hewitt et al. 1996), suggesting large-scale facilitation of invertebrate communities.

High abundances of living *Austrovenus* will also result in large depositions of dead shells in and on the sediments. For example, in 2009, there was a mass die-off in Whangateau Harbour, where a ca. 250 million *Austrovenus*, that is ca. 60% of the population, died (Jones et al. 2017) resulting in massive and rapid depositions of dead shells in a single estuary. Dead shells can thereby provide large-scale biogenic habitat in marine systems in New Zealand (Grange 1979, Greinert et al. 2010, South et al. 2017, see also Chapter 5) as seen in other places worldwide (Murray 1983, Gagné et al. 2008, Summerhayes et al. 2009, Ilarri et al. 2014). Here, I showed that these dead shells provided important habitat across latitudes, sites, and elevations (see Chapter 5 for more details).

Mobile snails and limpets were also surprisingly important habitat-formers across latitudes, sites, and elevations; including *Diloma nigerrimum, Micrelenchus huttonii, Amphibola crenata, Cominella glandiformis, Zeacumantus subcarinatus, Maoriculpus* spp., and *Lunella smaragda*. Very few studies have shown that large groups of snails can represent mobile communities of habitat-forming species (Thomsen et al. 2016). Here these snails (along with the limpet *Notoacmea* sp.) can be considered to be small moving islands of solitary hard substrate that increase biodiversity, and facilitate recruitment of sessile taxa (Suchanek 1992, Thomsen et al. 2007a, Wernberg et al. 2010, Thyrring et al. 2013, see also Chapters 5 and 6), potentially resulting in facilitation and habitat cascades (Altieri et al. 2007, Thomsen et al. 2010a, Angelini and Silliman 2014, Thomsen et al. 2016). Finally, I found that the encrusting bryozoan *Conopeum* (undescribed species, *pers. comm.* D. Gordon) also was an important habitat former. Little is known about this potentially non-native cryptic species (*pers. comm.* D. Gordon and see Thomsen et al. (2016)). Here I found that *Conopeum* often encrusted snails and bivalve shells where it converted smooth surfaces to rough textures for seaweed to settle on. Despite its small and cryptic appearance, this species may thereby be an ecologically important, but overlooked, species that link shell-formers and seaweed in 'long' habitat cascades (Thomsen et al. 2016).

Night vs. day and quadrat sizes

Contrary to my hypothesis, mobile organisms and their number of interactions did not differ between day and night samples. This result was unexpected because mobile species can

change behaviour with tidal elevation and/or show diurnal movements, as documented for several snails (Underwood 1979, Heiler et al. 2008), decapods (Burrows et al. 1999, Novak 2004), and limpets (Little 1989, Serra et al. 2001). Specifically, I expected that mobile snails and limpets would be more abundant in night samples (moving up from deeper waters or from within the sediment) because the risk from visual predators, like fish, crabs, and birds (Bisson 1978, Garrity and Levings 1981, Jacobsen and Stabell 1999), as well as heat and desiccation stress, is lower (Underwood 1979, Little 1989, Tomanek and Somero 1999). However, my results did not support this hypothesis. Instead, other factors may be more important than diurnal changes in predation risk or desiccation stress, such as water level (surveys were only done at low-tide) (Underwood 1979, Little 1989) or seasonal effects (Hamilton et al. 2003, Hodgson and Dickens 2012). Alternatively, it may be that mobile organisms in the Avon-Heathcote simply do not exhibit diurnal patterns in migration or burial.

Finally, I found, as would be expected from species-area curve theory (Connor and McCoy 1979, Palmer and White 1994), that richness of habitat-formers and habitat-users were higher in large than small samples. This result is also explained by island biogeography theory (Simberloff 1976, Connor and McCoy 1979, Palmer and White 1994) where large samples are more likely to include high spatial heterogeneity, more microclimates and high habitat diversity, than small samples. For example, in estuaries, the likelihood of encountering a mixture of habitat forming seagrass, dead shells, bryozoa, and different seaweed species, will increase with sample size, and thereby resulting in higher richness (Simberloff 1976, Kohn and Walsh 1994, and see Chapter 3). However, even though more taxa were in large samples, rarefaction curves showed higher sampling efficiency in small samples, that is, more species were counted, for the same area, in the small quadrats (Figure 4.9C, E). This higher sampling efficiency in small samples may reflect edge effects (it can be difficult to determine if a species is inside or outside a small quadrat) or that it is easier 'mentally' to identify all existing minuscule and cryptic interactions (with continued high concentration) in small samples. In general, the result for this habitat-interaction survey thereby supports conclusions from a review of marine benthic sampling methods Pringle (1984) that more, smaller, quadrat sizes are preferential to large quadrat sizes for sampling benthic substrates, to decrease labour intensity and required time to sample.

However, the mean number of habitat interactions, when converted to unit area, was unaffected by quadrat size. This result suggest that these types of relatively poorly described

species-interaction can be measured and compared between different ecosystems and sampling scales to match differences in organismal and patch size of a particular system.

Conclusions

My results provide strong evidence that biogenic habitat formation is an important process in estuarine benthic communities on the South Island of New Zealand. Importantly, many organisms, often overlooked as foundation species such as dead shells and small mobile snails and limpets, were among the most important habitat-formers. These conclusions were robust across latitudes, estuaries, elevation levels, sites, quadrat sizes, and sampling time. I suggest they are also representative for many other estuaries around the world and perhaps even for other marine systems where facilitation through habitat-formation have been shown to be important, such as coral reefs, mangroves, or rocky reefs.

Tables

Table 0.1 ANOVA testing for effects of latitudinal region (north, central, south) and tidal elevation (low, high) on (A) habitat interactions, (B) richness of habitat-formers, and (C) richness of habitat-users. Twelve quadrats (0.010 m^2) were sampled in each of 14 estuaries on the South Island of New Zealand. Significant effects are in bold.

Response	Test Factor	Df	SS	F-value	p
A. Habitat Interactions	**Region**	**2**	**7112202**	**3.577**	**0.030**
	Elevation	**1**	**5232166**	**5.263**	**0.023**
	Region×Elevation	2	1018249	0.512	0.600
	Residuals	162	161055886		
B. Habitat-Former Richness	**Region**	**2**	**34.2**	**7.098**	**0.001**
	Elevation	**1**	**13.7**	**5.687**	**0.018**
	Region×Elevation	2	2.2	0.465	0.629
	Residuals	162	390.6		
C. Habitat-User Richness	**Region**	**2**	**103.0**	**9.017**	**<0.001**
	Elevation	**1**	**97.5**	**17.076**	**<0.001**
	Region×Elevation	2	15.9	1.394	0.251
	Residuals	162	925.2		

Table 0.2 ANOVA testing for effects of habitat (mud, silt, sand, seagrass) and elevation (low, high) on (A) habitat interactions, (B) richness of habitat-formers, and (C) richness of habitat-users (log 10 transformed) in the Avon-Heathcote Estuary. This survey was done with large quadrats (0.0625 m^2, silty sites n = 21, sandy, muddy and seagrass sites n = 14). Significant effects are in bold.

Response	Test Factor	Df	SS	F-value	p
A. Habitat Interactions	Site	3	49303784	2.452	0.073
	Elevation	1	16056549	2.395	0.127
	Site×Elevation	3	8681366	0.432	0.731
	Residuals	55	368692601		
B. Habitat-Former Richness	**Site**	**3**	**38.08**	**3.948**	**0.013**
	Elevation	**1**	**13.76**	**4.280**	**0.043**
	Site×Elevation	3	1.63	0.169	0.917
	Residuals	55	176.85		
C. Habitat-User Richness	**Site**	**3**	**0.3862**	**3.143**	**0.032**
	Elevation	**1**	**0.2081**	**5.081**	**0.028**
	Site×Elevation	3	0.0017	0.014	0.998
	Residuals	55	2.2526		

Table 0.3 ANOVA testing for diurnal effects (day, night) on (A) habitat interactions involving mobile organisms, (B) richness of mobile habitat-formers, and (C) richness of mobile habitat-users. This survey was done with small quadrats (0.010 m^2, n = 8) near Plover street in the Avon-Heathcote estuary. Significant effects are in bold.

(A) Measure	Test Factor	Df	SS	F-value	p
A. Habitat Interactions	Time	1	722500	0.518	0.484
	Residuals	14	19537500		
B. Habitat-Former Richness	Time	1	1.562	1.423	0.253
	Residuals	14	15.375		
C. Habitat-User Richness	Time	1	0.062	0.044	0.837
	Residuals	14	19.875		

Table 0.4 ANOVA testing for effects of quadrat size (0.0625 m^2, 0.010 m^2) and habitat (mud, dead shells, seagrass) on (A) habitat interactions, (B) richness of habitat-formers, and (C) richness of habitat-users. This survey was done near Tern Street in the Avon-Heathcote estuary (n = 3 per combination of quadrat size and habitat). Significant effects are in bold.

Response	Test Factor	Df	SS	F-value	p
A. Habitat Interactions	Size	1	2663432	0.740	0.407
	Habitat	2	2128816	0.296	0.749
	Size×Habitat	**2**	**39581616**	**5.499**	**0.020**
	Residuals	12	43189152		
B. Habitat-Former Richness	**Size**	**1**	**16.056**	**16.056**	**0.002**
	Habitat	**2**	**12.111**	**6.056**	**0.015**
	Size×Habitat	2	0.778	0.389	0.686
	Residuals	12	12		
C. Habitat-User Richness	**Size**	**1**	**32.00**	**30.32**	**<0.001**
	Habitat	**2**	**25.33**	**12.00**	**0.001**
	Size×Habitat	**2**	**28.00**	**13.26**	**0.001**
	Residuals	12	12.67		

Figures

Figure 0.1 Site locations and names of estuaries sampled on the South Island of New Zealand in a latitudinal survey (left, middle) and various surveys in the Avon-Heathcote estuary (right) of benthic habitat-formers and habitat-users.

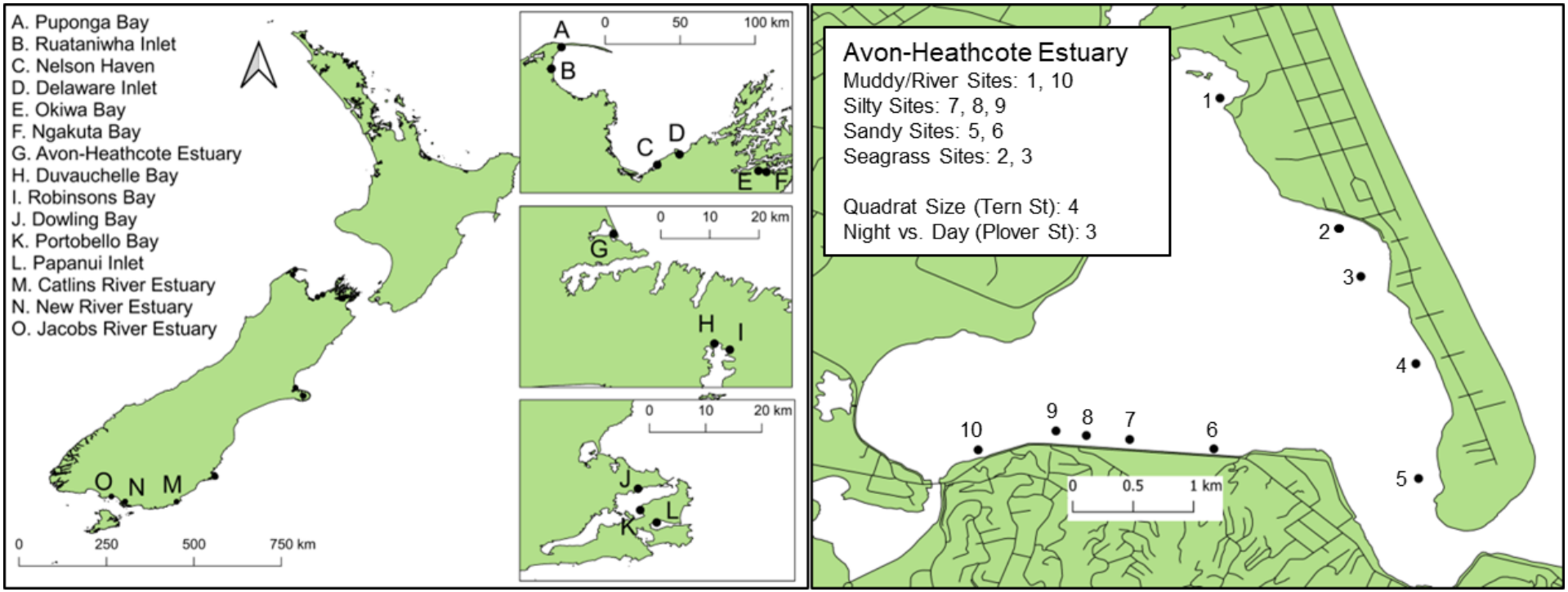


Figure 0.2 Percent cover (+SE) of benthic habitats types in 14 estuaries grouped into three latitudinal regions at (A) low and (B) high tidal elevation, on the South Island of New Zealand. Quadrat size = 0.010 m^2.

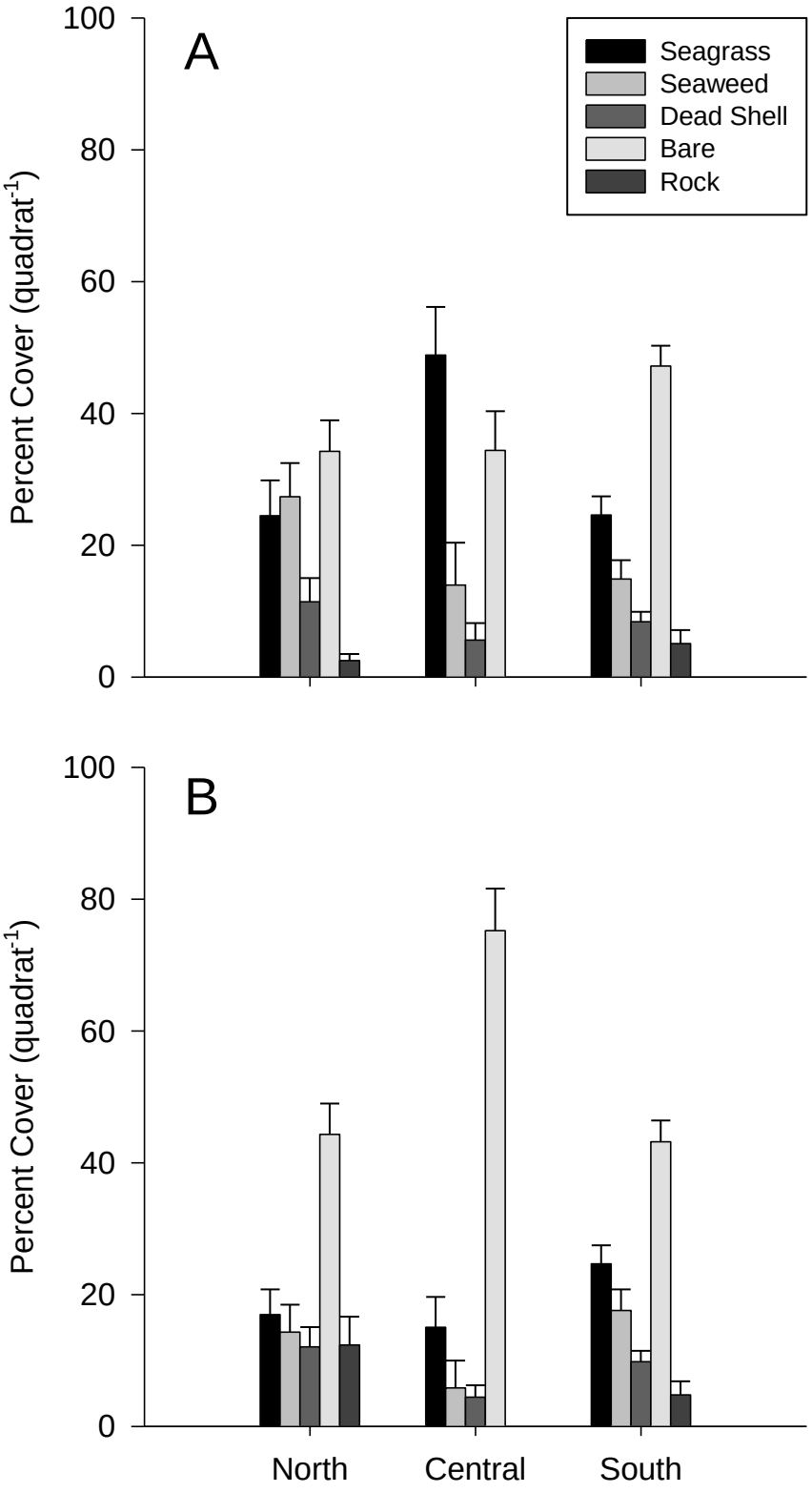


Figure 0.3 (A) Number (+SE) of habitat interactions (m^{-2}), (B) richness of habitat-formers and (C) richness of habitat-users in 14 estuaries grouped into three latitudinal regions at low and high elevation, on the South Island of New Zealand. Quadrat size = 0.010 m^2.

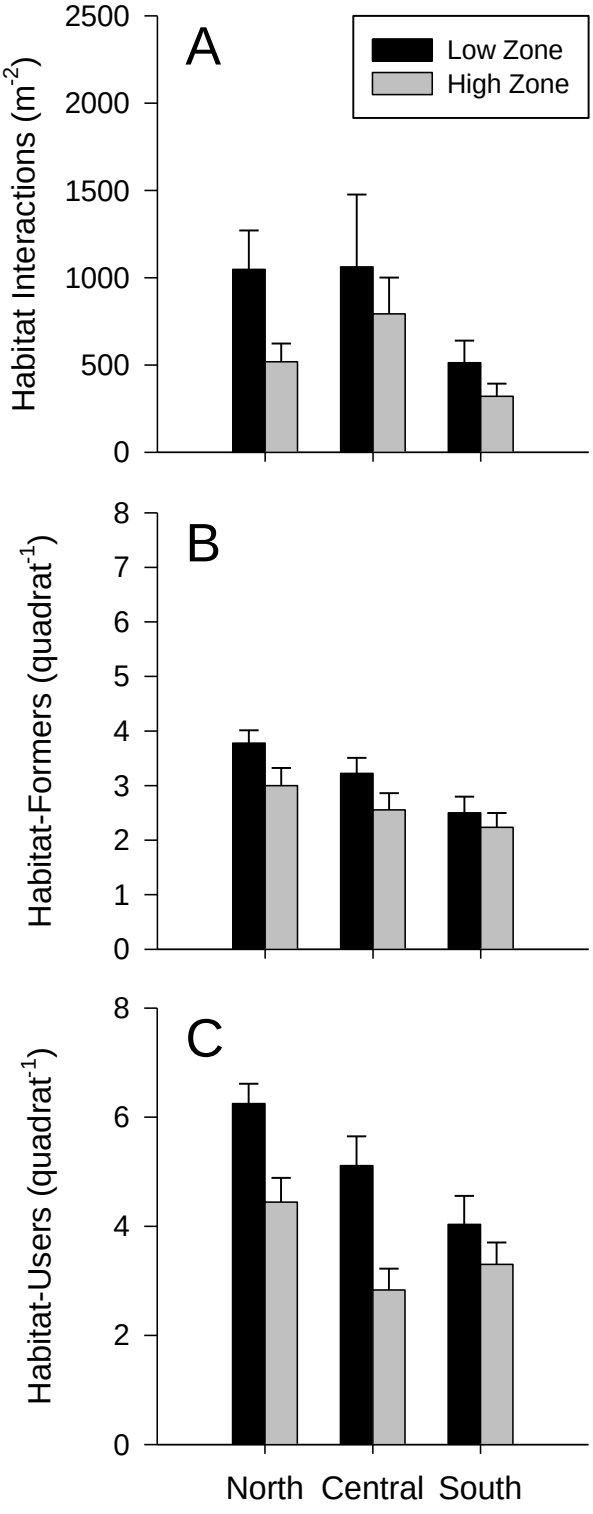
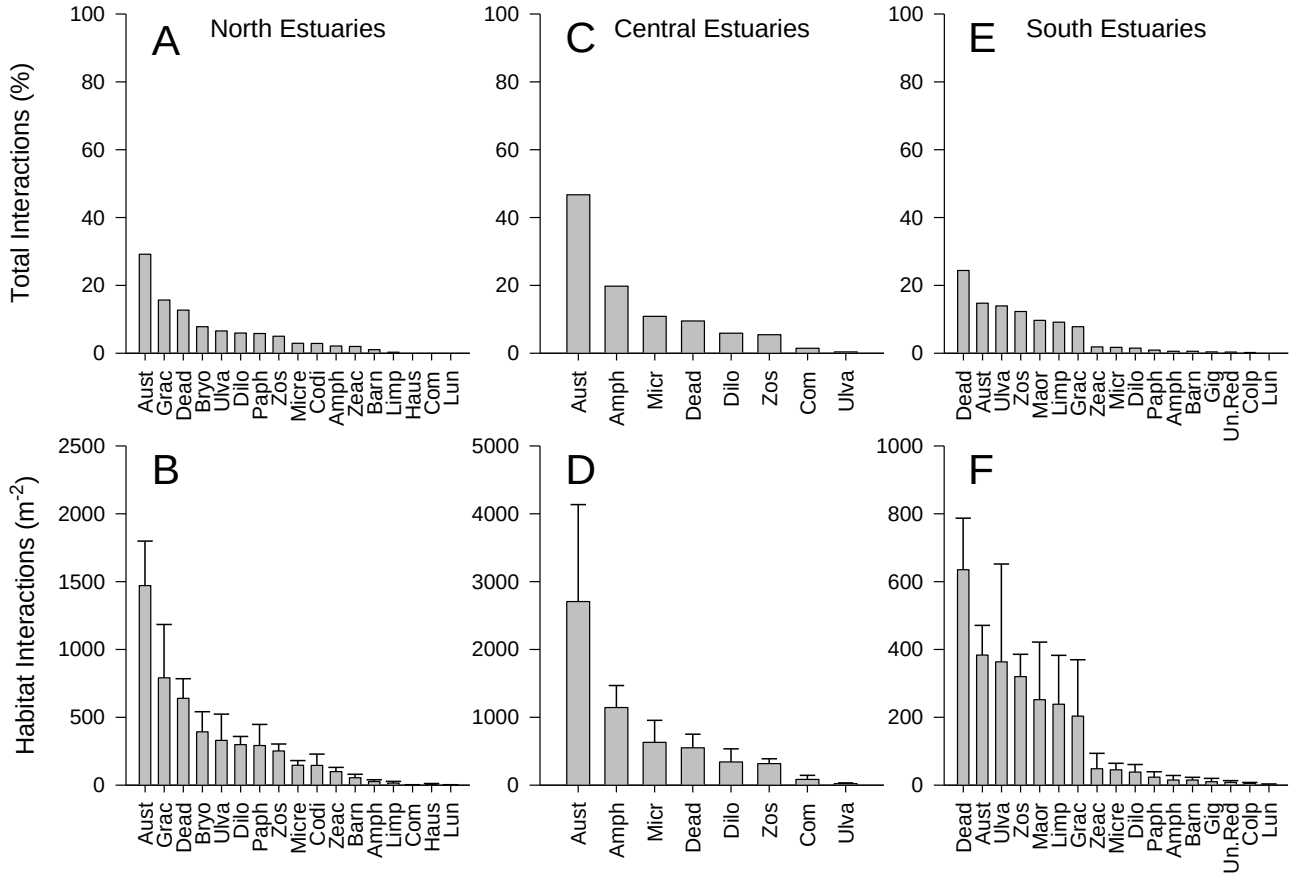


Figure 0.4 (A, C, E) Percentage of habitat-interactions for individual habitat-formers in 14 estuaries grouped into three latitudinal regions (the sum of all interactions in each region = 100%) on the South Island of New Zealand. (B, D, F) Number (+SE) of habitat interactions for individual habitat-formers (m^{-2}) across latitudinal regions. All data were pooled across two tidal elevation levels. Note scale differences on the y-axes. Quadrat size = 0.010 m^2.



Amph = *Amphibola crenata*, Aust = *Austrovenus stutchburyi*, Barn = Barnacles (unidentified), Bryo = Encrusting bryozoans (unidentified), Codi = *Codium fragile*, Colp = *Colpomenia bullosa*, Com = *Cominella glandiformis*, Dead = Dead shells, Dilo = *Diloma nigerrimum*, Gig = *Gigartina* spp., Grac = *Gracilaria chilensis*, Haus = *Haustrum haustorium*, Limp = *Notoacmea* spp., Lun = *Lunella smaragda*, Maor = *Maoriculpus* spp., Micre = *Micrelenchus huttonii*, Paph = *Paphies australis*, Ulva = *Ulva* spp., Un.Red = Red seaweed (unidentified), Zeac = *Zeacumantus subcarinatus*, Zos = *Zostera muelleri*

Figure 0.5 Percent cover (+SE) of benthic habitats types from sites with different environmental conditions at (A) low and (B) high tidal elevation, in the Avon-Heathcote Estuary. Quadrat size = 0.0625 m^2.

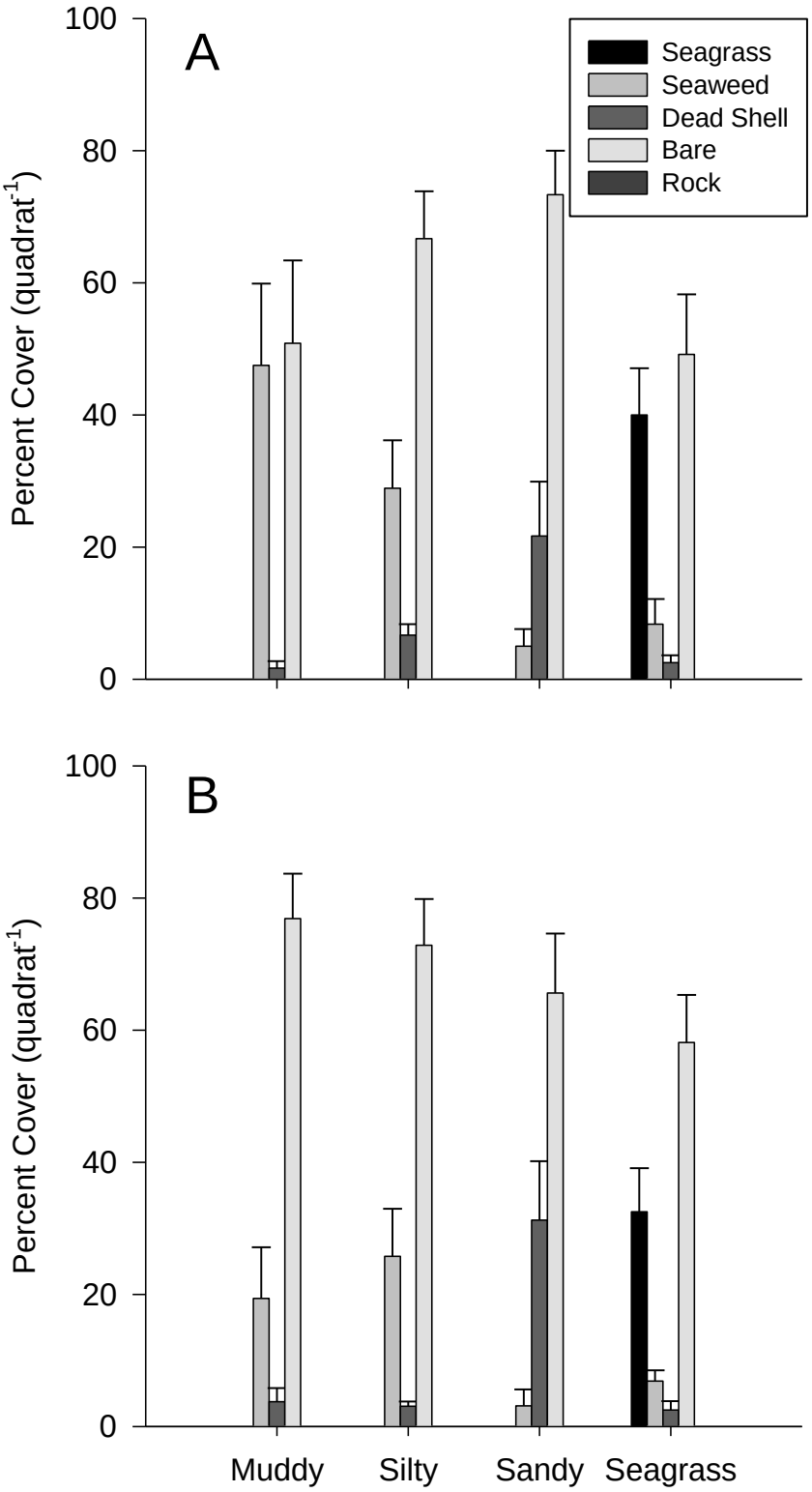


Figure 0.6 (A) Number (+SE) of habitat interactions (m^{-2}), (B) richness of habitat-formers and (C) richness of habitat-users from sites with different environmental conditions at low and high elevation, in the Avon-Heathcote Estuary. Quadrat size = 0.0625 m^2.

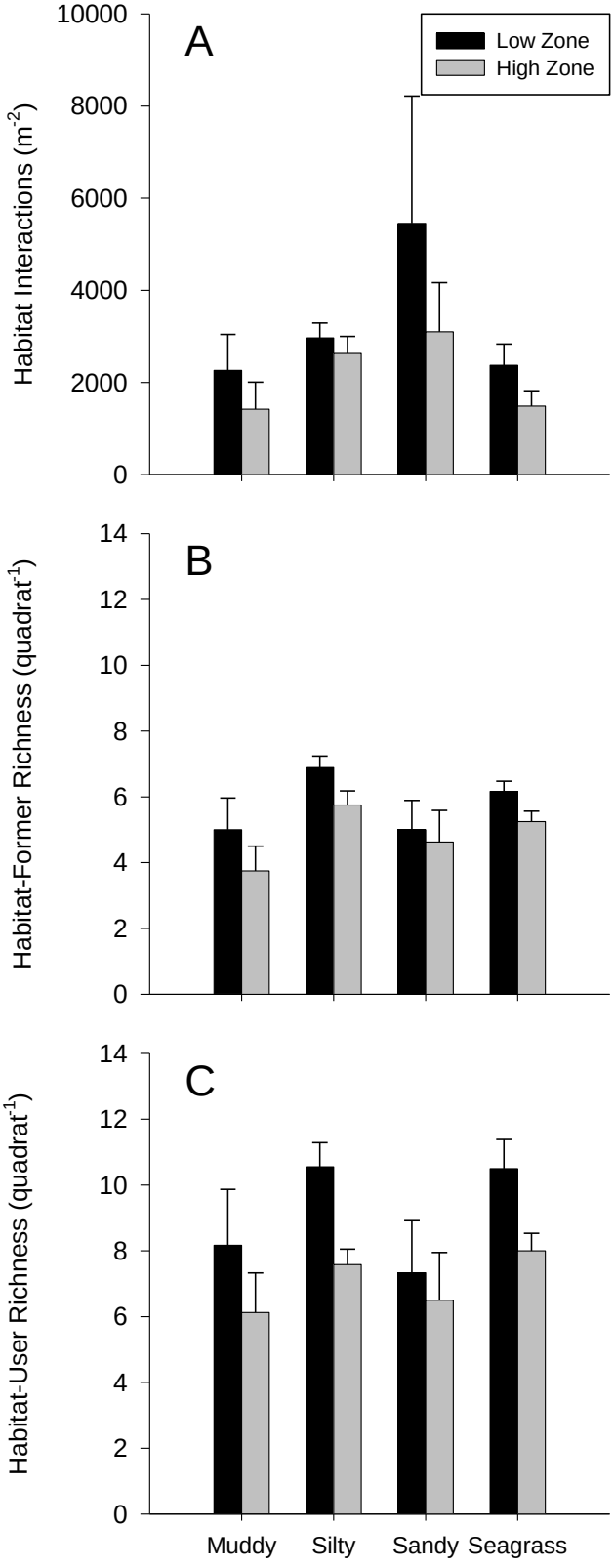
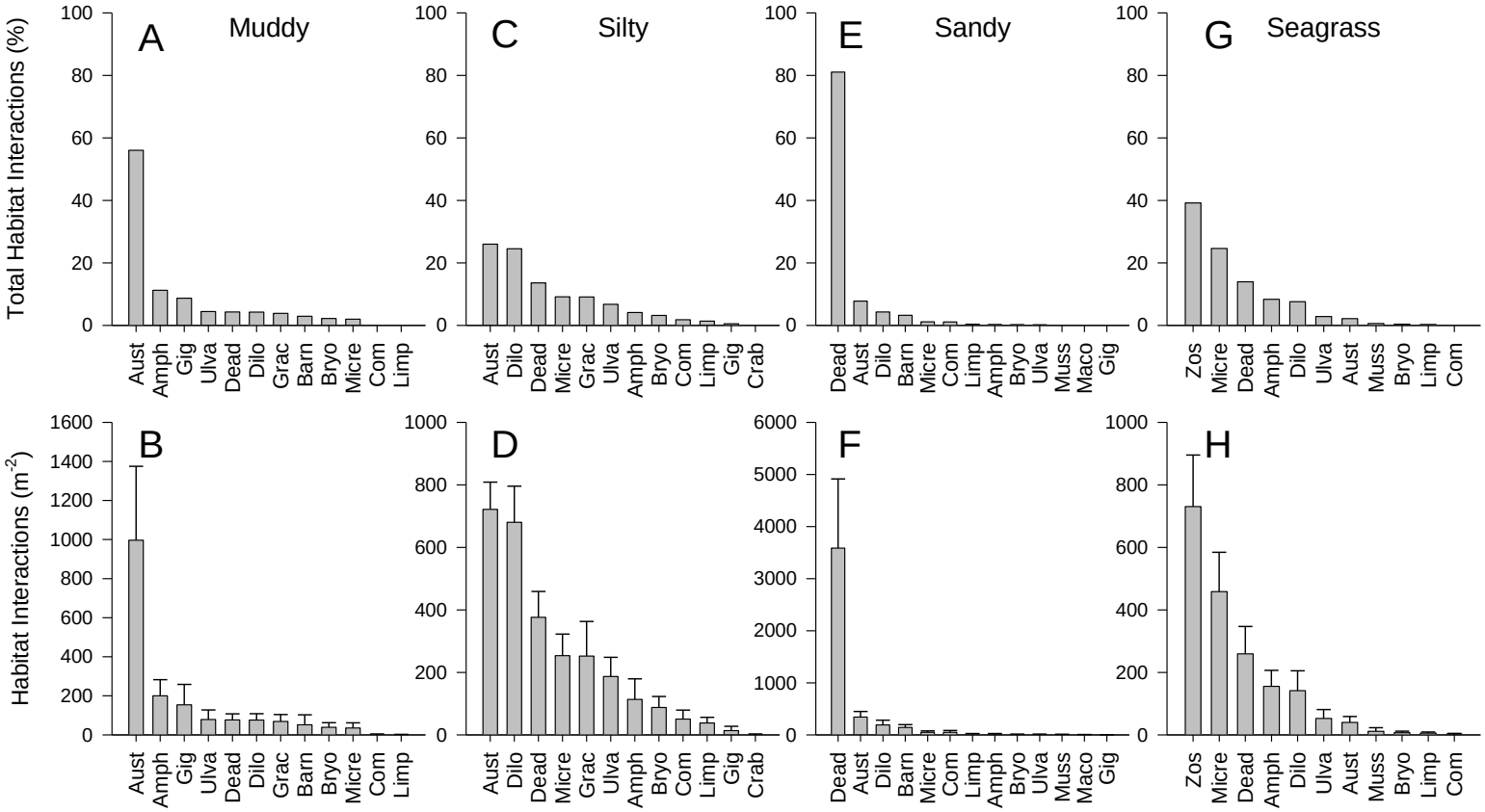


Figure 0.7 (A, C, E, G) Percentage of habitat-interactions for individual habitat-formers across sites with different environmental conditions (the sum of all interactions in each region = 100%) in the Avon Heathcote Estuary. (B, D, F, H) Number (+SE) of habitat interactions for individual habitat-formers (m^{-2}) across sites with different environmental conditions. All data were pooled across two tidal elevation levels. Note scale differences on the y-axes. Quadrat size = 0.0625 m^2.



Amph = *Amphibola crenata*, Aust = *Austrovenus stutchburyi*, Barn = Barnacles, Bryo = Encrusting bryozoans (*Conopeum* unid species), Com = *Cominella glandiformis*, Crab = *Austrohelice crassa*, Dead = Dead shells, Dilo = *Diloma nigerrimum*, Gig = *Gigartina* (unid species), Grac = *Gracilaria chilensis*, Limp = *Notoacmea* spp., Maco = *Macomona liliana*, Micre = *Micrelenchus huttonii*, Muss = *Mytilus edulis*, Ulva = *Ulva* spp., Zos = *Zostera muelleri*

Figure 0.8 (A) Number (+SE) of habitat interactions (m^{-2}), (B) richness of habitat-formers, and (C) richness of habitat-users, of mobile organisms in day or night samples, in a seagrass bed near Plover Street, in the Avon-Heathcote Estuary. Quadrat size = 0.010 m^2.

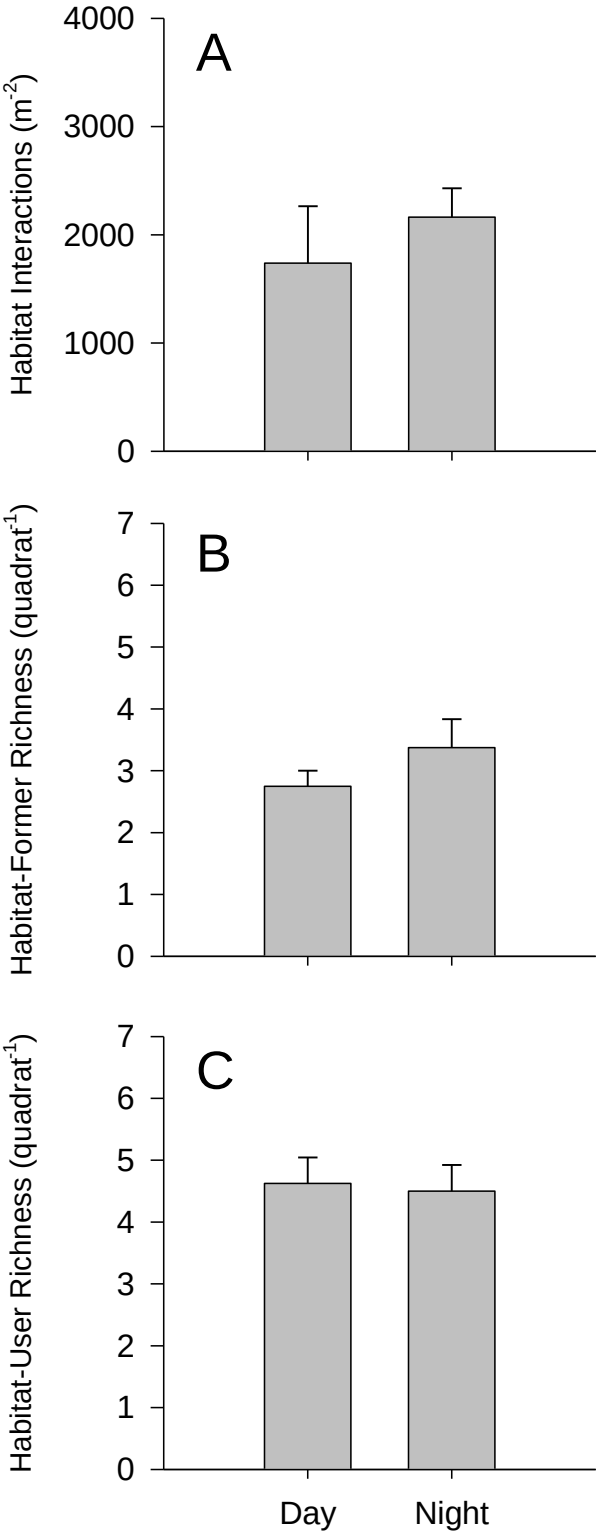
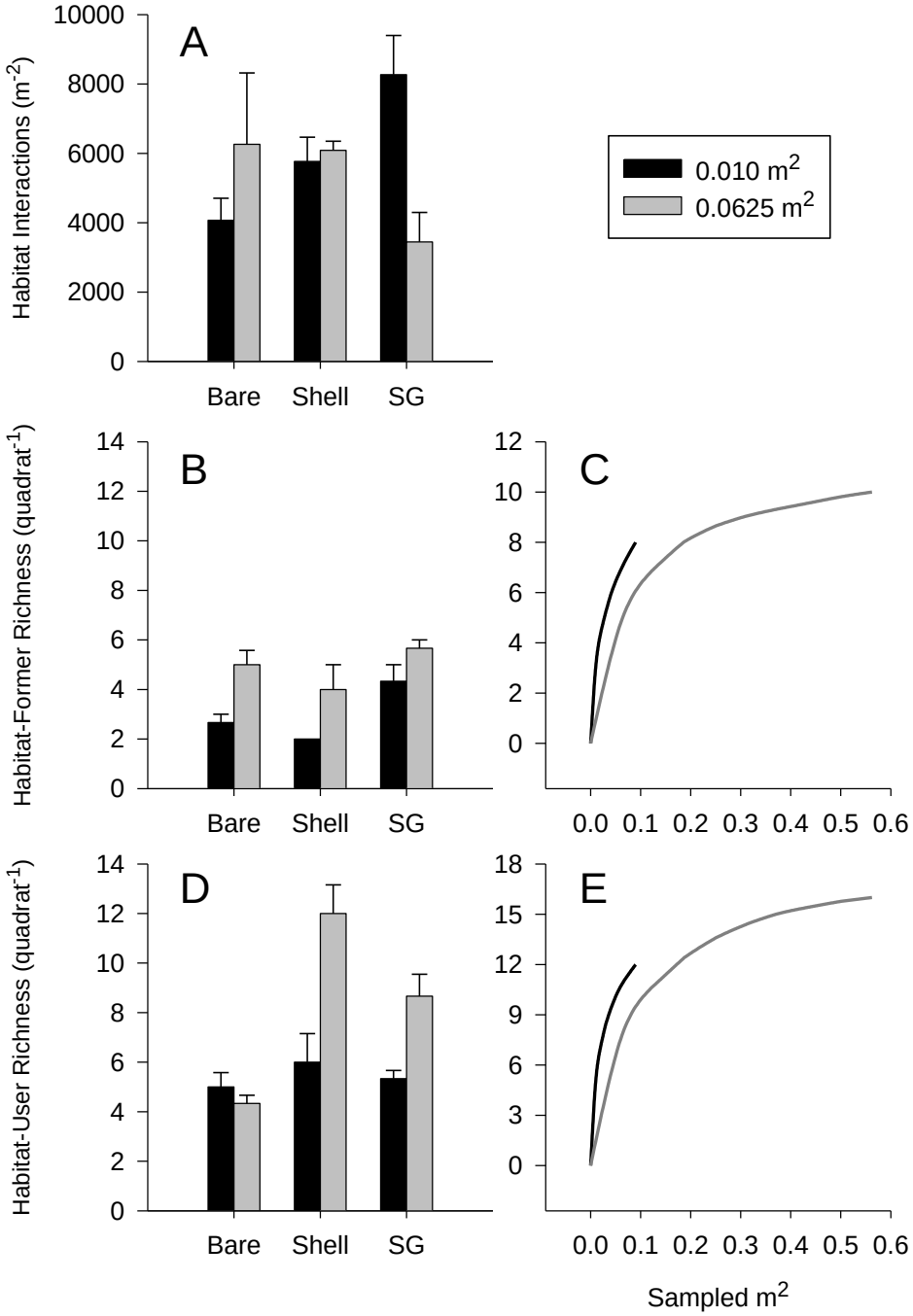


Figure 0.9 (A) Number (+SE) of habitat interactions (m^{-2}), (B, C) richness of habitat-formers, and (D, E) richness of habitat-users, in small (0.010 m^2) and large (0.0625 m^2) quadrats in habitats dominated by mud (Bare), dead shells (Shell) or seagrasses (SG) near Tern Street in the Avon-Heathcote Estuary (n = 3 for each combination of quadrate size and habitat). Associated species-area rarefaction curves of taxa richness for the small and large quadrats are shown in (C) for habitat-formers and (E) for habitat-users.



References

Ackerman, J. D. 1983. Specificity and mutual dependency of the orchid-euglossine bee interaction. Biological Journal of the Linnean Society **20**:301-314.

Airoldi, L. 2000. Responses of algae with different life histories to temporal and spatial variability of disturbance in subtidal reefs. Marine Ecology Progress Series **195**:81-92.

Albrecht, M., and Gotelli, N. J. 2001. Spatial and temporal niche partitioning in grassland ants. Oecologia **126**:134-141.

Alfaro, A. C. 2006. Benthic macro-invertebrate community composition within a mangrove/seagrass estuary in northern New Zealand. Estuarine, Coastal and Shelf Science **66**:97-110.

Allen, M. C., Read, A. J., Gaudet, J., and Sayigh, L. S. 2001. Fine-scale habitat selection of foraging bottlenose dolphins *Tursiops truncatus* near Clearwater, Florida. Marine Ecology Progress Series **222**:253-264.

Altieri, A. H., Silliman, B. R., and Bertness, M. D. 2007. Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. The American Naturalist **169**:195-206.

Altieri, A. H., and Witman, J. D. 2014. Modular mobile foundation species as reservoirs of biodiversity. Ecosphere **5**:1-11.

Angelini, C., Altieri, A. H., Silliman, B. R., and Bertness, M. D. 2011. Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. BioScience **61**:782-789.

Angelini, C., and Silliman, B. R. 2014. Secondary foundation species as drivers of trophic and functional diversity: Evidence from a tree–epiphyte system. Ecology **95**:185-196.

Angelini, C., van der Heide, T., Griffin, J. N., Morton, J. P., Derksen-Hooijberg, M., Lamers, L. P., Smolders, A. J., and Silliman, B. R. 2015. Foundation species' overlap enhances biodiversity and multifunctionality from the patch to landscape scale in southeastern United States salt marshes. Proceedings of the Royal Society B **282**:1-9.

Araújo, M. S., Guimarães, P. R., Svanbäck, R., Pinheiro, A., Guimarães, P., Reis, S. F. d., and Bolnick, D. I. 2008. Network analysis reveals contrasting effects of intraspecific competition on individual vs. population diets. Ecology **89**:1981-1993.

Aristotle. 1910. Historia animalium. Page 345 *in* D. A. W. Thompson, editor. A History of Animals. Clarendon Press, Oxford.

Asmala, E., Autio, R., Kaartokallio, H., Pitkänen, L., Stedmon, C. A., and Thomas, D. N. 2013. Bioavailability of riverine dissolved organic matter in three Baltic Sea estuaries and the effect of catchment land use. Biogeosciences **10**:6969-6986.

Atilla, N., Wetzel, M. A., and Fleeger, J. W. 2003. Abundance and colonization potential of artificial hard substrate-associated meiofauna. Journal of Experimental Marine Biology and Ecology **287**:273-287.

Attrill, M. J., Stafford, R., and Rowden, A. A. 2001. Latitudinal diversity patterns in estuarine tidal flats: indications of a global cline. Ecography **24**:318-324.

Ballance, L. T. 1992. Habitat use patterns and ranges of the bottlenose dolphin in the Gulf of California, Mexico. Marine Mammal Science **8**:262-274.

Banks, S. C., Piggott, M. P., Williamson, J. E., Bové, U., Holbrook, N. J., and Beheregaray, L. B. 2007. Oceanic variability and coastal topography shape genetic structure in a long-dispersing sea urchin. Ecology **88**:3055-3064.

Barber, I., Hoare, D., and Krause, J. 2000. Effects of parasites on fish behaviour: A review and evolutionary perspective. Reviews in Fish Biology and Fisheries **10**:131-165.

Barker, G. 2005. The character of the New Zealand landsnail fauna and communities: some evolutionary and ecological perspectives.

Battley, P. F., Melville, D. S., Schuckard, R., and Ballance, P. F. 2011. *Zostera muelleri* as a structuring agent of benthic communities in a large intertidal sandflat in new zealand. Journal of Sea Research **65**:19-27.

Beekey, M. A., McCabe, D. J., and Marsden, J. E. 2004. Zebra mussel colonisation of soft sediments facilitates invertebrate communities. Freshwater Biology **49**:535-545.

Bellingham, P. J., Stewart, G. H., and Allen, R. B. 1999. Tree species richness and turnover throughout New Zealand forests. Journal of Vegetation Science **10**:825-832.

Bishop, M. J., Byers, J. E., Marcek, B. J., and Gribben, P. E. 2012. Density-dependent facilitation cascades determine epifaunal community structure in temperate Australian mangroves. Ecology **93**:1388-1401.

Bisson, P. A. 1978. Diel food selection by two sizes of rainbow trout (*Salmo gairdneri*) in an experimental stream. Journal of the Fisheries Research Board of Canada **35**:971-975.

Boström, C., Jackson, E. L., and Simenstad, C. A. 2006. Seagrass landscapes and their effects on associated fauna: a review. Estuarine, Coastal and Shelf Science **68**:383-403.

Brun, F. G., Zetten, E., Cacabelos, E., and Bouma, T. J. 2009. Role of two contrasting ecosystem engineers (*Zostera noltii* and *Cymodocea nodosa*) on the food intake rate of *Cerastoderma edule*. Helgoland Marine Research **63**:19-25.

Bulleri, F., Airoldi, L., Branca, G. M., and Abbiati, M. 2006. Positive effects of the introduced green alga, *Codium fragile* ssp. *tomentosoides*, on recruitment and survival of mussels. Marine Biology **148**:1213-1220.

Burrows, M. T., Kawai, K., and Hughes, R. N. 1999. Foraging by mobile predators on a rocky shore: Underwater tv observations of movements of blennies *Lipophrys pholis* and crabs *Carcinus maenas*. Marine Ecology Progress Series **187**:237-250.

Carpenter, S. R., Kitchell, J. F., and Hodgson, J. R. 1985. Cascading trophic interactions and lake productivity. BioScience **35**:634-639.

Carr, J., D'Odorico, P., McGlathery, K., and Wiberg, P. 2010. Stability and bistability of seagrass ecosystems in shallow coastal lagoons: role of feedbacks with sediment resuspension and light attenuation. Journal of Geophysical Research: Biogeosciences **115**:1-14.

Chiswell, S. M., and Rickard, G. J. 2011. Larval connectivity of harbours via ocean currents: a New Zealand study. Continental Shelf Research **31**:1057-1074.

Chiswell, S. M., and Schiel, D. R. 2001. Influence of along-shore advection and upwelling on coastal temperature at Kaikoura Peninsula, New Zealand. New Zealand Journal of Marine and Freshwater Research **35**:307-317.

Colwell, M. A., and Landrum, S. L. 1993. Nonrandom shorebird distribution and fine-scale variation in prey abundance. The Condor **95**:94-103.

Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology **42**:710-723.

Connolly, R. M., and Hindell, J. S. 2006. Review of nekton patterns and ecological processes in seagrass landscapes. Estuarine, Coastal and Shelf Science **68**:433-444.

Connor, E. F., and McCoy, E. D. 1979. The statistics and biology of the species-area relationship. The American Naturalist **113**:791-833.

Cusson, M., and Bourget, E. 2005. Small-scale variations in mussel (*Mytilus* spp.) dynamics and local production. Journal of Sea Research **53**:255-268.

Dauer, D., Tourtellotte, G., and Ewing, R. 1982. Oyster shells and artificial worm tubes: The role of refuges in structuring benthic communities of the lower Chesapeake Bay. Internationale Revue der Gesamten Hydrobiologie und Hydrographie **67**:661-677.

Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. Pages 81-96 *in* Proceedings of the colloquium on conservation problems in Antarctica. Allen Press Lawrence, Kansas, USA.

Dean, R. L., and Connell, J. H. 1987. Marine invertebrates in an algal succession III. Mechanisms linking habitat complexity with diversity. Journal of Experimental Marine Biology and Ecology **109**:249-273.

Dickson, J. G., and Noble, R. E. 1978. Vertical distribution of birds in a Louisiana bottomland hardwood forest. The Wilson Bulletin **90**:19-30.

Dijkstra, J. A., Harris, L. G., Mello, K., Litterer, A., Wells, C., and Ware, C. 2017. Invasive seaweeds transform habitat structure and increase biodiversity of associated species. Journal of Ecology **105**:1668-1678.

Donadi, S., van der Heide, T., Piersma, T., van der Zee, E. M., Weerman, E. J., van de Koppel, J., Olff, H., Devine, C., Hernawan, U. E., Boers, M., Planthof, L., and Klemens Eriksson, B. 2015. Multi-scale habitat modification by coexisting ecosystem engineers drives spatial separation of macrobenthic functional groups. Oikos **124**:1502-1510.

Drouin, A., McKindsey, C. W., and Johnson, L. E. 2011. Higher abundance and diversity in faunal assemblages with the invasion of *Codium fragile* ssp. *fragile* in eelgrass meadows. Marine Ecology Progress Series **424**:105-117.

Duke, N., Ball, M., and Ellison, J. 1998. Factors influencing biodiversity and distributional gradients in mangroves. Global Ecology & Biogeography Letters **7**:27-47.

Ellison, A. M., Bank, M. S., Clinton, B. D., Colburn, E. A., Elliott, K., Ford, C. R., Foster, D. R., Kloeppel, B. D., Knoepp, J. D., and Lovett, G. M. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment **3**:479-486.

Engle, V. D., and Summers, J. K. 1999. Latitudinal gradients in benthic community composition in Western Atlantic estuaries. Journal of Biogeography **26**:1007-1023.

Fonseca, M. S., and Cahalan, J. A. 1992. A preliminary evaluation of wave attenuation by four species of seagrass. Estuarine, Coastal and Shelf Science **35**:565-576.

Foster, B. A. 1971. Desiccation as a factor in the intertidal zonation of barnacles. Marine Biology **8**:12-29.

Francis, M. P., Morrison, M. A., Leathwick, J., and Walsh, C. 2011. Predicting patterns of richness, occurrence and abundance of small fish in New Zealand estuaries. Marine and Freshwater Research **62**:1327-1341.

Francis, M. P., Morrison, M. A., Leathwick, J., Walsh, C., and Middleton, C. 2005. Predictive models of small fish presence and abundance in northern New Zealand harbours. Estuarine, Coastal and Shelf Science **64**:419-435.

Furey, N. B., Dance, M. A., and Rooker, J. R. 2013. Fine-scale movements and habitat use of juvenile southern flounder *Paralichthys lethostigma* in an estuarine seascape. Journal of Fish Biology **82**:1469-1483.

Gagné, F., Blaise, C., Pellerin, J., Fournier, M., Durand, M. J., and Talbot, A. 2008. Relationships between intertidal clam population and health status of the soft-shell clam *Mya arenaria* in the St. Lawrence Estuary and Saguenay Fjord (Québec, Canada). Environment International **34**:30-43.

Gain, I. E., Brewton, R. A., Reese Robillard, M. M., Johnson, K. D., Smee, D. L., and Stunz, G. W. 2016. Macrofauna using intertidal oyster reef varies in relation to position within the estuarine habitat mosaic. Marine Biology **164**:8.

Garrity, S. D., and Levings, S. C. 1981. A predator-prey interaction between two physically and biologically constrained tropical rocky shore gastropods: direct, indirect and community effects. Ecological Monographs **51**:267-286.

Genner, M. J., and Michel, E. 2003. Fine-scale habitat associations of soft-sediment gastropods at Cape Maclear, Lake Malawi. Journal of Molluscan Studies **69**:325-328.

Grange, K. R. 1979. Soft-bottom macrobenthic communities of Manukau Harbour, New Zealand. New Zealand Journal of Marine and Freshwater Research **13**:315-329.

Greinert, J., Lewis, K. B., Bialas, J., Pecher, I. A., Rowden, A., Bowden, D. A., De Batist, M., and Linke, P. 2010. Methane seepage along the Hikurangi Margin, New Zealand: overview of studies in 2006 and 2007 and new evidence from visual, bathymetric and hydroacoustic investigations. Marine Geology **272**:6-25.

Guidone, M., Newton, C., and Thornber, C. S. 2014. Utilization of the invasive alga *Gracilaria vermiculophylla* (Ohmi) Papenfuss by the native mud snail *Ilyanassa obsoleta* (Say). Journal of Experimental Marine Biology and Ecology **452**:119-124.

Gutiérrez, J. L., Jones, C. G., Strayer, D. L., and Iribarne, O. O. 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos **101**:79-90.

Hall, L. S., Krausman, P. R., and Morrison, M. L. 1997. The habitat concept and a plea for standard terminology. Wildlife Society Bulletin (1973-2006) **25**:173-182.

Hamilton, D. J., Barbeau, M. A., and Diamond, A. W. 2003. Shorebirds, mud snails, and *Corophium volutator* in the upper Bay of Fundy, Canada: predicting bird activity on intertidal mud flats. Canadian Journal of Zoology **81**:1358-1366.

Harley, C. D. G., and Helmuth, B. S. T. 2003. Local- and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation. Limnology and Oceanography **48**:1498-1508.

Harris, G. P. 2001. Biogeochemistry of nitrogen and phosphorus in australian catchments, rivers and estuaries: effects of land use and flow regulation and comparisons with global patterns. Marine and Freshwater Research **52**:139-149.

Hastie, B. F., and Smith, S. D. A. 2006. Benthic macrofaunal communities in intermittent estuaries during a drought: comparisons with permanently open estuaries. Journal of Experimental Marine Biology and Ecology **330**:356-367.

Heck, K. L., and Orth, R. J. 1980. Seagrass habitats: The roles of habitat complexity, competition and predation in structuring associated fish and motile invertebrate assemblages. Pages 449-464 *in* V. S. Kennedy, editor. Estuarine perspectives. Academic Press.

Heiler, K. C. M., Von Oheimb, P. V., Ekschmitt, K., and Albrecht, C. 2008. Studies on the temperature dependence of activity and on the diurnal activity rhythm of the invasive *Pomacea canaliculata* (Gastropoda: Ampullariidae). Mollusca **26**:73-81.

Herkül, K., and Kotta, J. 2009. Effects of eelgrass (*Zostera marina*) canopy removal and sediment addition on sediment characteristics and benthic communities in the northern Baltic Sea. Marine Ecology **30**:74-82.

Hewitt, J. E., Thrush, S. F., Cummings, V. J., and Pridmore, R. D. 1996. Matching patterns with processes: predicting the effect of size and mobility on the spatial distributions of the bivalves *Macomona liliana* and *Austrovenus stutchburyi*. Marine Ecology Progress Series **135**:57-67.

Hodgson, A. N., and Dickens, J. 2012. Activity of the mangrove snail *Cerithidea decollata* (Gastropoda: Potamididae) in a warm temperate South African estuary. Estuarine, Coastal and Shelf Science **109**:98-106.

Hollever, J., and Bolton-Ritchie, L. 2016. Broad scale mapping of the estuary of the Heathcote and Avon rivers/Ihutai. Environment Canterbury.

Huston, M. A. 1994. Biological diversity: The coexistence of species on changing landscapes. Cambridge University Press, Cambridge.

Ilarri, M. I., Souza, A. T., Antunes, C., Guilhermino, L., and Sousa, R. 2014. Influence of the invasive asian clam *Corbicula fluminea* (Bivalvia: Corbiculidae) on estuarine epibenthic assemblages. Estuarine, Coastal and Shelf Science **143**:12-19.

Inglis, G. 2003. Seagrasses of New Zealand. Pages 134-143 *in* E. P. Green and F. T. Short, editors. World atlas of seagrasses: Present status and future conservation. . University of California Press, Berkeley, California.

Irlandi, E., Orlando, B., and Biber, P. 2004. Drift algae-epiphyte-seagrass interactions in a subtropical *Thalassia testudinum* meadow. Marine Ecology Progress Series **279**:81-91.

Jacobs, S. W. L., Les, D. H., and Moody, M. L. 2006. New combinations in Australasian *Zostera* (Zosteraceae). Telopea **11**:127-128.

Jacobsen, H. P., and Stabell, O. B. 1999. Predator-induced alarm responses in the common periwinkle, *Littorina littorea*: dependence on season, light conditions, and chemical labelling of predators. Marine Biology **134**:551-557.

Jones, C. G., Lawton, J. H., and Shachak, M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology **78**:1946-1957.

Jones, H. F. E., Pilditch, C. A., Hamilton, D. P., and Bryan, K. R. 2017. Impacts of a bivalve mass mortality event on an estuarine food web and bivalve grazing pressure. New Zealand Journal of Marine and Freshwater Research **51**:370-392.

Jones, M. B. 1976. Limiting factors in the distribution of intertidal crabs (Crustacea: Decapoda) in the Avon-Heathcote Estuary, Christchurch. New Zealand Journal of Marine and Freshwater Research **10**:577-587.

Jones, T. C., Gemmill, C. E. C., and Pilditch, C. A. 2008. Genetic variability of New Zealand seagrass (*Zostera muelleri*) assessed at multiple spatial scales. Aquatic Botany **88**:39-46.

Kainamu-Murchie, A. A., Marsden, I. D., Tau, R. T. M., Gaw, S., and Pirker, J. 2018. Indigenous and local peoples' values of estuarine shellfisheries: Moving towards holistic-based catchment management. New Zealand Journal of Marine and Freshwater Research **52**:526-541.

Keeney, D. B., Szymaniak, A. D., and Poulin, R. 2013. Complex genetic patterns and a phylogeographic disjunction among New Zealand mud snails *Zeacumantus subcarinatus* and *Z. lutulentus*. Marine Biology **160**:1477-1488.

Koen, J. H. 1988. Stratal distribution and resource partitioning of birds in the Knysna Forest, South Africa. African Journal of Ecology **26**:229-238.

Kohn, D. D., and Walsh, D. M. 1994. Plant species richness-the effect of island size and habitat diversity. Journal of Ecology **82**:367-377.

Lamouroux, N., Capra, H., Pouilly, M., and Souchon, Y. 1999. Fish habitat preferences in large streams of southern France. Freshwater Biology **42**:673-687.

Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. The American Naturalist **134**:922-949.

Leung, T. L., and Poulin, R. 2007. Interactions between parasites of the cockle *Austrovenus stutchburyi*: hitch-hikers, resident-cleaners, and habitat-facilitators. Parasitology **134**:247-255.

Little, C. 1989. Factors governing patterns of foraging activity in littoral marine herbivorous molluscs. Journal of Molluscan Studies **55**:273-284.

Lowell, R. B. 1984. Desiccation of intertidal limpets: effects of shell size, fit to substratum, and shape. Journal of Experimental Marine Biology and Ecology **77**:197-207.

Macara, G. R. 2016. Regional climatologies.*in* NIWA, editor.

MacArthur, R. H., and Wilson, E. O. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J.

Marsden, I. D., and Bressington, M. J. 2009. Effects of macroalgal mats and hypoxia on burrowing depth of the New Zealand cockle (*Austrovenus stutchburyi*). Estuarine, Coastal and Shelf Science **81**:438-444.

Matheson, F. E., Lundquist, C. J., Gemmill, C. E. C., and Pilditch, C. A. 2011. New Zealand seagrass – more threatened than IUCN review indicates. Biological Conservation **144**:2749-2750.

Mayfield, M. M., Boni, M. F., Daily, G. C., and Ackerly, D. 2005. Species and functional diversity of native and human-dominated plant communities. Ecology **86**:2365-2372.

McClatchie, S., Millar, R. B., Webster, F., Lester, P. J., Hurst, R., and Bagley, N. 1997. Demersal fish community diversity off New Zealand: is it related to depth, latitude and regional surface phytoplankton? Deep Sea Research Part I: Oceanographic Research Papers **44**:647-667.

McGlone, P. S., Richardson, S. J., and Jordan, G. J. 2010. Comparative biogeography of New Zealand trees: species richness, height, leaf traits and range sizes. New Zealand Journal of Ecology **34**:137-151.

McLeod, I. M., Parsons, D. M., Morrison, M. A., Van Dijken, S. G., and Taylor, R. B. 2013. Mussel reefs on soft sediments: a severely reduced but important habitat for macroinvertebrates and fishes in New Zealand. New Zealand Journal of Marine and Freshwater Research **48**:48-59.

Menge, B. A., and Sutherland, J. P. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. The American Naturalist **130**.

Mills, V. S., and Berkenbusch, K. 2009. Seagrass (*Zostera muelleri*) patch size and spatial location influence infaunal macroinvertebrate assemblages. Estuarine, Coastal and Shelf Science **81**:123-129.

Mitchell, C. P. 1980. Intertidal distribution of six trochids at Portobello, New Zealand. New Zealand Journal of Marine and Freshwater Research **14**:47-54.

Moreno-Rueda, G. 2006. Habitat use by the arid-dwelling land snail *Iberus g. gualtieranus*. Journal of Arid Environments **67**:336-342.

Morris, D. W. 1987. Ecological scale and habitat use. Ecology **68**:362-369.

Mouritsen, K. N. 2002. The parasite-induced surfacing behaviour in the cockle *Austrovenus stutchburyi*: a test of an alternative hypothesis and identification of potential mechanisms. Parasitology **124**.

Mouritsen, K. N., and Poulin, R. 2003. The mud flat anemone-cockle association: mutualism in the intertidal zone? Oecologia **135**:131-137.

Mouritsen, K. N., and Poulin, R. 2006. A parasite indirectly impacts both abundance of primary producers and biomass of secondary producers in an intertidal benthic community. Journal of the Marine Biological Association of the UK **86**:221.

Munari, C., Bocchi, N., and Mistri, M. 2015. Epifauna associated to the introduced *Gracilaria vermiculophylla* (Rhodophyta; Florideophyceae: Gracilariales) and comparison with the native *Ulva rigida* (Chlorophyta; Ulvophyceae: Ulvales) in an Adriatic lagoon. Italian Journal of Zoology **82**:436-445.

Murray, J. W. 1983. Population dynamics of benthic Foraminifera; results from the Exe Estuary, England. The Journal of Foraminiferal Research **13**:1-12.

Mvungi, E. F., Lyimo, T. J., and Björk, M. 2012. When *Zostera marina* is intermixed with *Ulva*, its photosynthesis is reduced by increased pH and lower light, but not by changes in light quality. Aquatic Botany **102**:44-49.

Nadrowski, K., Wirth, C., and Scherer-Lorenzen, M. 2010. Is forest diversity driving ecosystem function and service? Current Opinion in Environmental Sustainability **2**:75-79.

Naugle, D. E., Higgins, K. F., Nusser, S. M., and Johnson, W. C. 1999. Scale-dependent habitat use in three species of prairie wetland birds. Landscape Ecology **14**:267-276.

NIWA. 2016. New Zealand annual climate summary: 2016. *in* N.I.W.A. Research.

Novak, M. 2004. Diurnal activity in a group of Gulf of Maine decapods. Crustaceana **77**:603-620.

Olesen, J. M., and Jordano, P. 2002. Geographic patterns in plant–pollinator mutualistic networks. Ecology **83**:2416-2424.

Orth, R. J., Carruthers, T. J., Dennison, W. C., Duarte, C. M., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., and Olyarnik, S. 2006. A global crisis for seagrass ecosystems. BioScience **56**:987-996.

Orth, R. J., Heck, K. L., and van Montfrans, J. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries **7**:339-350.

Overton, J. M., Barker, G. M., and Price, R. 2009. Estimating and conserving patterns of invertebrate diversity: a test case of New Zealand land snails. Diversity and Distributions **15**:731-741.

Pacala, S. W., and Roughgarden, J. 1985. Population experiments with the anolis lizards of St. Maarten and St. Eustatius. Ecology **66**:129-141.

Palmer, M. W., and White, P. S. 1994. Scale dependence and the species-area relationship. The American Naturalist **144**:717-740.

Peterson, C. H. 1991. Intertidal zonation of marine invertebrates in sand and mud. American Scientist **79**:236-249.

Peterson, M. S. 2003. A conceptual view of environment-habitat-production linkages in tidal river estuaries. Reviews in Fisheries Science **11**:291-313.

Price, P. W., Bouton, C. E., Gross, P., McPheron, B. A., Thompson, J. N., and Weis, A. E. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. Annual review of ecology and systematics **11**:41-65.

Pringle, C. M., Naiman, R. J., Bretschko, G., Karr, J. R., Oswood, M. W., Webster, J. R., Welcomme, R. L., and Winterbourn, M. J. 1988. Patch dynamics in lotic systems: the stream as a mosaic. Journal of the North American Benthological Society **7**:503-524.

Pringle, J. D. 1984. Efficiency estimates for various quadrat sizes used in benthic sampling. Canadian Journal of Fisheries and Aquatic Sciences **41**:1485-1489.

Queiroz, R. N. M., and Dias, T. L. P. 2014. Molluscs associated with the macroalgae of the genus *Gracilaria* (Rhodophyta): importance of algal fronds as microhabitat in a hypersaline mangrove in northeastern Brazil. Brazilian Journal of Biology **74**:S052-S063.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raffaelli, D. G., Raven, J. A., and Poole, L. J. 1998. Ecological impact of green macroalgal blooms. Oceanography and Marine Biology: an annual review **36**:97-125.

Ramus, A. P., Silliman, B. R., Thomsen, M. S., and Long, Z. T. 2017. An invasive foundation species enhances multifunctionality in a coastal ecosystem. Proceedings of the National Academy of Sciences **114**:8580-8585.

Rasmussen, J. R., Pedersen, M. F., Olesen, B., Nielsen, S. L., and Pedersen, T. M. 2013. Temporal and spatial dynamics of ephemeral drift-algae in eelgrass, *Zostera marina*, beds. Estuarine, Coastal and Shelf Science **119**:167-175.

Ricciardi, A., Whoriskey, F. G., and Rasmussen, J. B. 1997. The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. Canadian Journal of Fisheries and Aquatic Sciences **54**:2596-2608.

Richardson, J. R., Aldridge, A. E., and Main, W. d. L. 1979. Distribution of the New Zealand cockle *Chione stutchburyi* at Pauatahanui Inlet. New Zealand Oceanographic Institute.

Rosenfeld, S., Aldea, C., Mansilla, A., Marambio, J., and Ojeda, J. 2015. Richness, systematics, and distribution of molluscs associated with the macroalga *Gigartina skottsbergii* in the Strait of Magellan, Chile: A biogeographic affinity study. ZooKeys **519**.

Ross, P. M., Hogg, I. D., Pilditch, C. A., and Lundquist, C. J. 2009. Phylogeography of New Zealand's coastal benthos. New Zealand Journal of Marine and Freshwater Research **43**:1009-1027.

Rountree, R. A., and Able, K. W. 2007. Spatial and temporal habitat use patterns for salt marsh nekton: implications for ecological functions. Aquatic Ecology **41**:25-45.

Ruiz, G. M., Freestone, A. L., Fofonoff, P. W., and Simkanin, C. 2009. Habitat distribution and heterogeneity in marine invasion dynamics: the importance of hard substrate and artificial structure. Pages 321-332 *in* M. Wahl, editor. Marine hard bottom communities: Patterns, dynamics, diversity, and change. Springer Berlin Heidelberg, Berlin, Heidelberg.

Rybarczyk, H., and Elkaïm, B. 2003. An analysis of the trophic network of a macrotidal estuary: the Seine Estuary (Eastern Channel, Normandy, France). Estuarine, Coastal and Shelf Science **58**:775-791.

Saint-Béat, B., Dupuy, C., Agogué, H., Carpentier, A., Chalumeau, J., Como, S., David, V., De Crignis, M., Duchêne, J.-C., Fontaine, C., Feunteun, E., Guizien, K., Hartmann, H., Lavaud, J., Lefebvre, S., Lefrançois, C., Mallet, C., Montanié, H., Mouget, J.-L., Orvain, F., Ory, P., Pascal, P.-Y., Radenac, G., Richard, P., Vézina, A. F., and Niquil, N. 2014. How does the resuspension of the biofilm alter the functioning of the benthos–pelagos coupled food web of a bare mudflat in Marennes-Oléron Bay (NE Atlantic)? Journal of Sea Research **92**:144-157.

Sandwell, D. R., Pilditch, C. A., and Lohrer, A. M. 2009. Density dependent effects of an infaunal suspension-feeding bivalve (*Austrovenus stutchburyi*) on sandflat nutrient fluxes and microphytobenthic productivity. Journal of Experimental Marine Biology and Ecology **373**:16-25.

Sanford, E., and Kelly, M. W. 2011. Local adaptation in marine invertebrates. Annual Review of Marine Science **3**:509-535.

Schiel, D. R. 2011. Biogeographic patterns and long-term changes on New Zealand coastal reefs: non-trophic cascades from diffuse and local impacts. Journal of Experimental Marine Biology and Ecology **400**:33-51.

Schmidt, A. L., Coll, M., Romanuk, T. N., and Lotze, H. K. 2011. Ecosystem structure and services in eelgrass *Zostera marina* and rockweed *Ascophyllum nodosum* habitats. Marine Ecology Progress Series **437**:51-68.

Schmidt, A. L., and Scheibling, R. E. 2006. A comparison of epifauna and epiphytes on native kelps (*Laminaria* species) and an invasive alga (*Codium fragile* ssp. *tomentosoides*) in Nova Scotia, Canada. Botanica Marina **46**:315-330.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science **185**:27-39.

Seed, R. 1996. Patterns of biodiversity in the macro-invertebrate fauna associated with mussel patches on rocky shores. Journal of the Marine Biological Association of the United Kingdom **76**:203-210.

Serra, G., Chelazzi, G., and Castilla, J. C. 2001. Temporal and spatial activity of the key-hole limpet fissurella crassa (mollusca: Gastropoda) in the eastern pacific. Journal of the Marine Biological Association of the United Kingdom **81**:485-490.

Shumway, S. E., and Marsden, I. d. 1982. The combined effects of temperature, salinity, and declining oxygen tension on oxygen consumption in the marine pulmonate amphibola crenata (gmelin, 1791). Journal of Experimental Marine Biology and Ecology **61**:133-146.

Simberloff, D. 1976. Experimental zoogeography of islands: effects of island size. Ecology **57**:629-648.

Smith, T. J., and Duke, N. C. 1987. Physical determinants of inter-estuary variation in mangrove species richness around the tropical coastline of Australia. Journal of Biogeography **14**:9-19.

Snyder, E. J., and Best, L. B. 1988. Dynamics of habitat use by small mammals in prairie communities. The American Midland Naturalist **119**:128-136.

South, P. M., Floerl, O., and Jeffs, A. G. 2017. Differential effects of adult mussels on the retention and fine-scale distribution of juvenile seed mussels and biofouling organisms in long-line aquaculture. Aquaculture Environment Interactions **9**:239-256.

Stachowicz, J. J. 2001. Mutualism, facilitation, and the structure of ecological communities. BioScience **51**:235-246.

Stouffer, D. B., Cirtwill, A. R., and Bascompte, J. 2014. How exotic plants integrate into pollination networks. Journal of Ecology **102**:1442-1450.

Suchanek, T. H. 1992. Extreme biodiversity in the marine-environment-mussel bed communities of *Mytilus californianus*. Northwest Environmental Journal **8**:150-152.

Summerhayes, S. A., Bishop, M. J., Leigh, A., and Kelaher, B. P. 2009. Effects of oyster death and shell disarticulation on associated communities of epibiota. Journal of Experimental Marine Biology and Ecology **379**:60-67.

Thomas, F., Poulin, R., de Meeüs, T., Guégan, J.-F., and Renaud, F. 1999. Parasites and ecosystem engineering: what roles could they play? Oikos **84**:167-171.

Thomas, F., Renaud, F., de Meeûs , T., and Poulin, R. 1998. Manipulation of host behaviour by parasites: ecosystem engineering in the intertidal zone? Proceedings of the Royal Society of London. Series B: Biological Sciences **265**:1091-1096.

Thomsen, M., Stæhr, P., Nejrup, L., and Schiel, D. 2013. Effects of the invasive macroalgae *Gracilaria vermiculophylla* on two co-occurring foundation species and associated invertebrates. Aquatic Invasions **8**:133-145.

Thomsen, M. S., de Bettignies, T., Wernberg, T., Holmer, M., and Debeuf, B. 2012. Harmful algae are not harmful to everyone. Harmful Algae **16**:74-80.

Thomsen, M. S., Hildebrand, T., South, P. M., Foster, T., Siciliano, A., Oldach, E., and Schiel, D. R. 2016. A sixth-level habitat cascade increases biodiversity in an intertidal estuary. Ecology and Evolution **6**:8291-8303.

Thomsen, M. S., Ramus, A. P., Long, Z. T., and Silliman, B. R. 2019. A seaweed increases ecosystem multifunctionality when invading bare mudflats. Biological Invasions **21**:27-36.

Thomsen, M. S., Silliman, B. R., and McGlathery, K. J. 2007. Spatial variation in recruitment of native and invasive sessile species onto oyster reefs in a temperate soft-bottom lagoon. Estuarine, Coastal and Shelf Science **72**:89-101.

Thomsen, M. S., and Wernberg, T. 2014. On the generality of cascading habitat-formation. Proceedings of the Royal Society B: Biological Sciences **281**:20131994.

Thomsen, M. S., and Wernberg, T. 2015. The devil in the detail: harmful seaweeds are not harmful to everyone. Global Change Biology **21**:1381-1382.

Thomsen, M. S., Wernberg, T., Altieri, A., Tuya, F., Gulbransen, D., McGlathery, K. J., Holmer, M., and Silliman, B. R. 2010. Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. Integrative and Comparative Biology **50**:158-175.

Thrush, S. F., Hewitt, J. E., Gibbs, M., Lundquist, C., and Norkko, A. 2006. Functional role of large organisms in intertidal communities: community effects and ecosystem function. Ecosystems **9**:1029-1040.

Thyrring, J., Thomsen, M. S., and Wernberg, T. 2013. Large-scale facilitation of a sessile community by an invasive habitat-forming snail. Helgoland Marine Research **67**:789-794.

Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology **75**:2-16.

Tomanek, L., and Somero, G. N. 1999. Evolutionary and acclimation-induced variation in the heat-shock responses of congeneric marine snails (genus *Tegula*) from different thermal habitats: implications for limits of thermotolerance and biogeography. The Journal of experimental biology **202**:2925-2936.

Turner, S., and Schwarz, A.-M. 2006. Management and conservation of seagrass in New Zealand: an introduction. Science for Conservation 264:1-90.

Tylianakis, J. M., Tscharntke, T., and Klein, A.-M. 2006. Diversity, ecosystem function, and stability of parasitoid–host interactions across a tropical habitat gradient. Ecology **87**:3047-3057.

Underwood, A. J. 1979. The ecology of intertidal gastropods. Pages 111-210 *in* F. S. Russell and M. Yonge, editors. Advances in marine biology. Academic Press.

van Houte-Howes, K. S. S., Turner, S. J., and Pilditch, C. A. 2004. Spatial differences in macroinvertebrate communities in intertidal seagrass habitats and unvegetated sediment in three New Zealand estuaries. Estuaries **27**:945-957.

Virnstein, R. W., and Carbonara, P. A. 1985. Seasonal abundance and distribution of drift algae and seagrasses in the Mid-Indian River Lagoon, Florida. Aquatic Botany **23**:67-82.

Wahl, M. 1996. Fouled snails in flow: Potential of epibionts on *Littorina littorea* to increase drag and reduce snail growth rates. Marine Ecology Progress Series **138**:157-168.

Ward, K. M., Callaway, J. C., and Zedler, J. B. 2003. Episodic colonization of an intertidal mudflat by native cordgrass (*Spartina foliosa*) at Tijuana Estuary. Estuaries **26**:116-130.

Watson, D. M., and Herring, M. 2012. Mistletoe as a keystone resource: an experimental test. Proceedings of the Royal Society of London B: Biological Sciences:rspb20120856.

Wernberg, T., Thomsen, M. S., and Kotta, J. 2013. Complex plant–herbivore–predator interactions in a brackish water seaweed habitat. Journal of Experimental Marine Biology and Ecology **449**:51-56.

Wernberg, T., Tuya, F., Thomsen, M. S., and Kendrick, G. 2010. Turban snails as habitat for foliose algae: contrasting geographical patterns in species richness. Marine and Freshwater Research **61**:1237-1242.

Whitlatch, R. B., Hines, A. H., Thrush, S. F., Hewitt, J. E., and Cummings, V. 1997. Benthic faunal responses to variations in patch density and patch size of a suspension-feeding bivalve. Journal of Experimental Marine Biology and Ecology **216**:171-189.

Williams, l., Cryer, M., McKenzie, l., Smith, M. D., Watson, T. G., MacKay, G., and Tasker, R. 2006. Biomass survey and stock assessment of cockles (A*ustrovenus stutchburyi*) on Snake Bank, Whangarei Harbour, 2005. *in* N.I.W.A. Research.

Wilson, K. A., Able, K. W., and Heck Jr., K. L. 1990. Predation rates on juvenile blue crabs in estuarine nursery habitats: evidence for the importance of macroalgae (*Ulva lactuca*). Marine Ecology Progress Series **58**:243-251.

Woods, C. M. C., and Schiel, D. R. 1997. Use of seagrass *Zostera novazelandica* (Setchell, 1933) as habitat and food by the crab *Macrophthalmus hirtipes* (Heller, 1862) (Brachyura: Ocypodidae) on rocky intertidal platforms in southern New Zealand. Journal of Experimental Marine Biology and Ecology **214**:49-65.

Wright, J. T., Byers, J. E., DeVore, J. L., and Sotka, E. E. 2014. Engineering or food? Mechanisms of facilitation by a habitat-forming invasive seaweed. Ecology **95**:2699-2706.

Wright, J. T., Byers, J. E., Koukoumaftsis, L. P., Ralph, P. J., and Gribben, P. E. 2010. Native species behaviour mitigates the impact of habitat-forming invasive seaweed. Oecologia **163**:527-534.

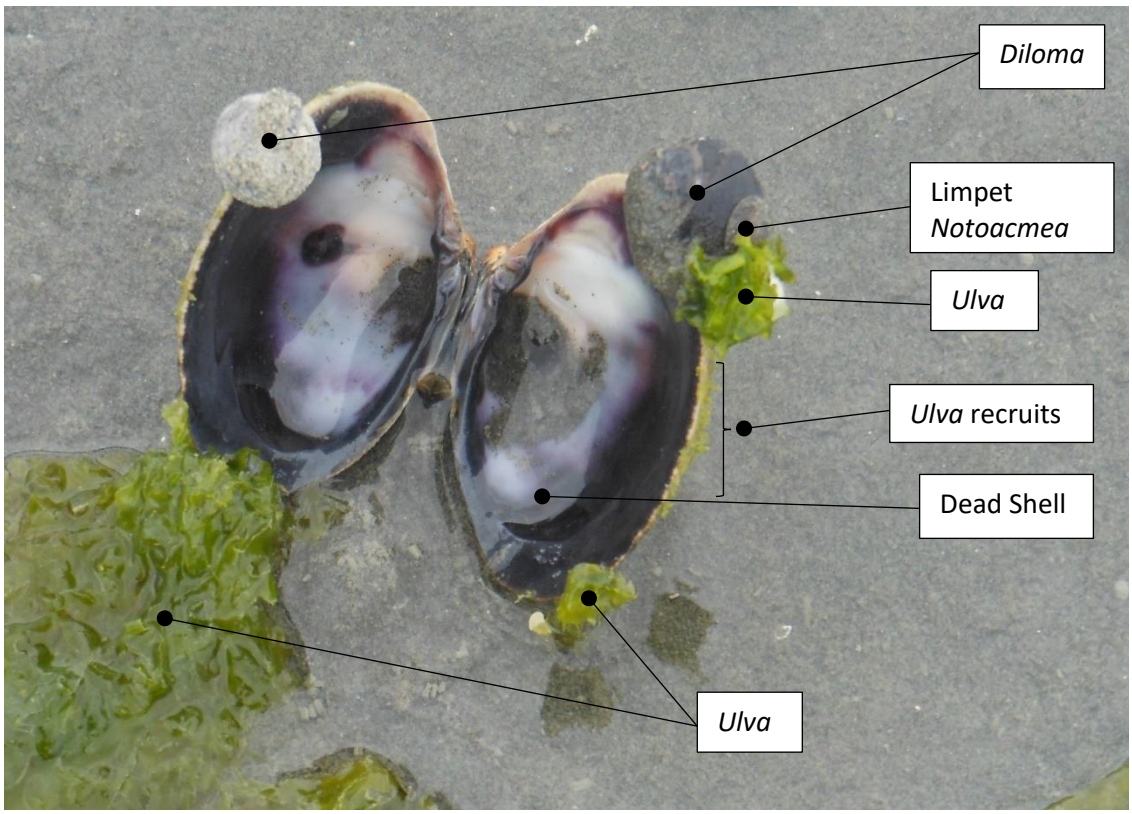
Yakovis, E., and Artemieva, A. 2017. Cockles, barnacles and ascidians compose a subtidal facilitation cascade with multiple hierarchical levels of foundation species. Scientific Reports **7**:237.

Yanoviak, S. P., and Kaspari, M. 2003. Community structure and the habitat templet: ants in the tropical forest canopy and litter. Oikos **89**:259-266.

Supplementary material

Example of how habitat-use was quantified (photo from the Avon-Heathcote Estuary, chosen for visualization; it was not from a quadrat sample). First, attachments of conspicuous mobile organisms were quantified (here *Diloma* and the limpet *Notoacmea*). The two *Diloma* snails (habitat-users) were both attached to a dead shell (habitat-former) representing 2 *Diloma*-Dead Shell habitat-interactions. In addition, one of the *Diloma* snails provide habitat to a limpet (=1 Limpet-*Diloma* interaction). An *Ulva* is also growing on the limpet (=1 *Ulva*-Limpet interaction) and on a dead shell (large green sheets as well as many small recruits attached to the lips of the shell). The number of *Ulva* holdfasts were counted to 15 (= 2 larger *Ulva* plus 13 small recruits along the edge). *Diloma* and other shells would be picked up to examine in detail possible inconspicuous habitat- interactions (not done here). In total, this photo contains

- 19 habitat interactions
    - 2 *Diloma*/Dead Shell
    - 1 Limpet/*Diloma*
    - 1 *Ulva*/Limpet
    - 15 *Ulva*/Dead Shell
- 3 Habitat-Formers (Richness)
    - Dead Shell
    - *Diloma*
    - Limpet
- 3 Habitat-Users (Richness)
    - *Diloma*
    - Limpet
    - *Ulva*



CHAPTER 5 DEAD SHELLS AS FOUNDATION SPECIES: LEGACY EFFECTS FROM AN ESTUARINE BIVALVE IN NEW ZEALAND

Abstract

Foundation species, such as the shell-forming *Austrovenus stutchburyi*, a common bivalve in New Zealand estuaries, are ecologically important organisms that facilitate many other organisms by modifying and enhancing the habitat around them. Many studies have documented the positive effects of living bivalves on benthic communities, but few studies have tested whether these effects persist after the bivalve has died, that is, if remaining shell structures leave 'ecological legacies'. The aim of this study was to quantify distribution patterns and test for effects of dead *Austrovenus* shells on benthic communities across latitudes, estuaries, habitats, and seasons, on the South Island of New Zealand. Distribution surveys showed that dead shells were present in all six sampled estuaries across three latitudinal regions (0.2-30% cover), at all four sampled sites within a single estuary (5.6-30% cover), and in both summer and winter seasons over multiple years at two of these four sites (4.3-17.8% cover). Furthermore, densities and taxonomic richness of invertebrates in the Avon-Heathcote Estuary were orders of magnitude greater in quadrats containing dead shells than in quadrats covering bare sediments. These results were supported by a shell-addition experiment carried out in the six surveyed estuaries; densities and taxonomic richness of invertebrates were again much higher (5× and 2×, respectively) in shell-addition treatments than on bare sediment control plots. I conclude that shells are common in New Zealand estuaries where they continue to provide habitat and hard substratum to benthic communities after the death of the bivalve, thereby creating hotspots of biodiversity. Dead shells should therefore be included in future estuarine research, conservation, and restoration plans.

Introduction

Foundation species are ecologically important organisms that facilitate biological communities via habitat creation, biological and physical stress reduction, and control of population dynamics (Dayton 1972, Ellison et al. 2005). These ecologically important organisms have been studied in great detail across ecosystems and habitats (e.g. Jones et al. 1994, 1997, Gilad et al. 2004, Ellison et al. 2005) albeit sometimes referred to as autogenic ecosystem engineers, structural species, keystone structures, or habitat-formers and modifiers

(Ellison et al. 2005, Thomsen et al. 2010a). The majority of this extensive literature has studied facilitation associated with living foundation species (e.g. Ellison et al. 2005, Altieri and Witman 2014, Angelini et al. 2015). However, facilitation processes can potentially continue after a foundation species has died. Such 'legacy effects' on resident communities can occur days, weeks, months, and even centuries past the organism's death (Hastings et al. 2007). These legacy effects have also been referred to as 'taphonomic feedbacks', particularly when and where habitat is provided by dead organisms (Kidwell and Jablonski 1983). Legacy effects may be important across spatio-temporal scales, environmental conditions, and from the assemblage level to an entire ecosystem. For example, beavers act as ecosystem modifiers on the landscape scale by building dams that change rivers into wetlands that may persist for centuries, even if beavers become locally extinct (Jones et al. 1994). Trees probably have one of the best known and most prominent structural legacy effects, as dead trees can continue to provide habitat to insects, birds and many other animals (Harmon et al. 1986, Franklin et al. 1987, Bunnell et al. 2002), promote forest regeneration (de Chantal and Granström 2007, Schlawin and Zahawi 2008), and affect soils and streams (Sedell and Froggatt 1984, Harmon et al. 1986, Franklin et al. 1987, Gregory et al. 1991).

The ecological importance of bivalves is particularly striking in sedimentary marine and estuarine systems where bivalve shells, alive or dead, provide hard-substrate and increase heterogeneity (Jones et al. 1994, Gutiérrez et al. 2003, Sousa et al. 2009). Many organisms are fundamentally dependent on these 'islands of hard substrate' for settling and colonization where they increase local biodiversity (Posey et al. 1999, Lehnert and Allen 2002, Gutiérrez et al. 2003, Tolley and Volety 2005, Grabowski and Peterson 2007, Schejter and Bremec 2007, Gribben et al. 2009, Brett et al. 2011, Thomsen et al. 2016). In addition, bivalves can also produce hard substrates in communities dominated by other foundation species such as salt marshes (Bertness 1984, Hacker and Gaines 1997, Altieri et al. 2007, Angelini et al. 2015), mangroves (Nagelkerken et al. 2008, Bishop et al. 2009, Bishop et al. 2013, Aquino-Thomas and Proffitt 2014), and seagrass beds (Irlandi 1997, Peterson and Heck Jr 2001b, Munguia 2007, Hendriks et al. 2011, Carroll and Peterson 2013, Thomsen et al. 2016, Gribben et al. 2017) which can further increase biodiversity. Bivalves, such as oysters, clams, mussels, and pen shells are particularly important aquatic foundation species, that can provide legacy effects through their calcium carbonate shells (Strayer and Malcom 2007). These shells persist in the environment long after the organism has died, sometimes for millions of years, as documented in marine fossil deposits (Kidwell 1986, Hastings et al. 2007, Strayer

and Malcom 2007). Marine bivalves can produce up to 90 kg shell material $m^{-2} \cdot year^{-1}$ (Beukema 1982, Powell et al. 1989), and deposit this hard substrate at a rate comparable to wood production in trees (Gutiérrez et al. 2003). Bivalves are widely distributed in aquatic systems and produce these persistent shells in a variety of habitats, such as streams, lakes, ponds, rocky shores, the deep ocean, hydrothermal vents, and many types of sedimentary marine systems from wave-exposed sandy beaches to protected inlets and estuaries (Strayer et al. 1999, Gutiérrez et al. 2003, Coen et al. 2011).In aquatic systems, dead seaweed and seagrass can provide legacy effects, such as when beached 'wrack' provide food or habitat for macrofauna, birds, and microalgae for days, weeks, and months after the seagrass and seaweed have died (Colombini and Chellazi 2003, Dugan et al. 2003, Rodil et al. 2008, Olabarria et al. 2010). However, long-lasting legacy effects are likely more important for aquatic calcifying organisms that build hard biogenic structures that can persist for centuries or even millennia. For example, many reef-building calcifying organisms, including corals, oysters, seaweed, mussels, and tube worms, are facilitated by previous generations dying off and creating hard substrate for new juveniles to settle onto (Kirtley and Tanner 1968, Bak 1976, Dame 1979, Jaap 2000, Lehnert and Allen 2002, Coen et al. 2007, Callaway et al. 2010, Gain et al. 2016).

Interactions between living bivalves and seagrasses have been studied in some detail (e.g., Chapter 1 and 2). For example, seagrasses provide settlement habitat for bivalve spat and adults (Reusch and Chapman 1995, Bologna and Heck 2000, Bologna et al. 2005), reduce predator foraging efficiency (Coen and Heck Jr. 1991, Irlandi and Peterson 1991, Beal 1994, Bologna and Heck 1999), and can enhance survival and growth (Irlandi 1996, Irlandi 1997, Irlandi et al. 1999, Boström et al. 2006). Similarly, bivalves can increase light penetration into seagrass beds (Newell and Koch 2004, Wall et al. 2008), provide nutrients (Reusch et al. 1994) and can reduce sulphide stress via symbiotic gill bacteria (van der Heide et al. 2012). However, not all bivalve-seagrass interactions are positive. For example, bivalves can compete with seagrass for space (Reusch and Williams 1998, Tallis et al. 2009, Wagner et al. 2012), physical abrasion from shells can lead to reduced desiccation tolerance at low-tides (Shreffler and Griffin 2000), and bio-deposits can over-enrich sediments (Vinther and Holmer 2008, Vinther et al. 2008). Finally, if seagrass strongly reduces water flow, filter-feeding bivalves can become food limited (Tsai et al. 2010). After the bivalve dies, some of these effects likely continue as long as the shell persists, such as competition for space and physical abrasion (Shreffler and Griffin 2000, Wagner et al. 2012).

Dead shells can affect both living organisms and abiotic characteristics of the environment.. For example, dead oyster shells facilitate settlement of juvenile oysters by providing chemical-cues and hard substrate for settlement and have been applied to restore deteriorated oyster reefs (Abbe 1988, Lehnert and Allen 2002, Waldbusser et al. 2011). Furthermore, dead shells reduce water acidity through their decomposition (Strayer and Malcom 2007, Waldbusser et al. 2011, Waldbusser et al. 2013), and act as long-term carbon sink, a process that slows down anthropogenic climate changes (Wilbur 1972, McConnaughey and Gillikin 2008, Schöne et al. 2011). Calcium shells (living and dead) are threatened through ocean acidification, which may dissolve the shells, hurting the many facilitative processes that occur (McClintock et al. 2009, Welladsen et al. 2010, Gaylord et al. 2011, Parker et al. 2013). To date, most research on legacy effects in aquatic systems have focused on how a few groups, such as dead oysters, pen shells, and zebra mussels, affect benthic invertebrate communities (Dauer et al. 1982, Ricciardi et al. 1997, Eggleston et al. 1999, Horvath et al. 1999, Lehnert and Allen 2002, Tolley and Volety 2005, Munguia 2007).

The objectives of this chapter are to quantify dead surface shells (a) within and among estuaries and (2) test how dead-shells affect benthic communities compared to unvegetated or seaweed- or seagrass-dominated habitats. To address the first objective three supplementary surveys were carried out comparing the abundance of surface-dwelling dead shells to common benthic estuarine habitats. To address the second objective, I compared invertebrate communities collected from quadrats with shells to quadrats of other benthic habitats, and tested, in a shell-addition experiment, for effects of dead shells on invertebrates in mudflats and in seagrass beds. I hypothesized that surface dwelling dead shells:

1. are common across estuaries, latitudes, sites, and seasons on the South Island of New Zealand, providing facilitative legacy effects to estuarine communities.
2. have positive effects on invertebrates and seaweed recruits, compared to unvegetated mudflats (similar to other biogenic habitats like seagrass and seaweed that are known to buffer stress)
3. have negative effects on seagrass, through competition for space and scouring of leaves.

Methods

Study sites

To assess the distribution of dead shells around the South Island of New Zealand, six estuaries were visited in summer (Oct-Feb) 2016/2017, representing two northern (Nelson Haven (41°13'51.4"S 173°18'33.4"E), Delaware Bay (41°10'05.6"S 173°26'33.6"E)), two central (Avon-Heathcote Estuary (43°33'09.3"S 172°44'40.5"E), Duvauchelle Bay (43°45'11.0"S 172°55'45.0"E)), and two southern (Portobello Bay (45°49'21.6"S 170°39'58.3"E), Papanui Inlet (45°50'32.7"S 170°41'33.0"E)) estuaries (Figure 5.1A). These estuaries were chosen because they are tidal, had extensive seagrass beds, were shallow with sandy to muddy sediments, and had gentle slopes. Additional surveys were carried out in the Avon-Heathcote Estuary (Figure 5.1B) to examine small scale spatio-temporal variation of dead shells. The Avon-Heathcote Estuary is surrounded by the city of Christchurch, New Zealand, and is an ca. 8.8 km^2 shallow, well-flushed, bar-built estuary. Two rivers flow into the estuary; the Avon River flows from the north and the Heathcote from the southwest (Figure 5.1B). Seagrass beds are abundant along the eastern side of the estuary where they cover ca. 0.35 km^2 (Hollever and Bolton-Ritchie 2016).

Distributions of dead shells in estuaries

Survey 1: Distribution of shells among estuaries and latitudes

A latitudinal survey was carried out to assess the distribution of surface dwelling shells across the six estuaries within the three latitudinal regions. Digital photographs were taken 90 cm from and perpendicular to the substratum, with a Nikon Coolpix AW100 camera, using a standardized method previously ground-truthed to unit area with transect-tapes (Thomsen et al. 2018a). Photographs were taken ca. every 2 m during low tide, by walking a straight transect line from the shore to the water's edge, thereby sampling all benthic habitats encountered on this transect. Transects were chosen in proximity to seagrass beds. Photographs (n = 90 per estuary) were analysed visually for percent cover of surface shells and other types of habitats, including sediment, seagrass, seaweeds, and rock, with a maximum cover of 100%, so if a seaweed covered a shell, only the seaweed was quantified. This rapid-sampling methodology is therefore a conservative estimate of shell abundances.

Survey 2: Distribution of dead shells in silt and seagrass habitats

A survey was carried out in the Avon Heathcote Estuary in December 2014 to January 2015 to estimate variability in percent cover of dead shells in two habitat types: silty (no seagrass)

and in seagrass beds, at four intertidal sites, Plover Street and Tern Street (seagrass), and Oxidation Ponds and Causeway (silty). Random photographs (Plover *n*=28, Tern *n*=57, Ponds *n*=75, Causeway *n*=88) were taken perpendicular to the substratum at each site, with each photograph covering ca. 1 m^2 as in Survey 1. Habitats were assessed as described for Survey 1.

Survey 3: Temporal distribution of dead shells

Finally, a survey was done to estimate temporal variability in cover of surface shells, by revisiting Plover Street and Tern Street eight times over two years from 2014-2016. Photographs were taken perpendicular to the substratum as described for the latitudinal survey. Photographs (n = 90 for each sample time) were analysed for percent cover of shells and other habitat-forming organisms as described for Survey 1.

Statistical analysis

Percent cover values were normalised by arcsine square-root transformation, followed by analysis of variance (ANOVA) to test whether benthic cover varied among regions and estuaries (Survey 1), habitat and sample sites (Survey 2) and season and sample sites (Survey 3). Homogeneity of variance was checked with Levene's test (package *'car'*). If variance homogeneity assumptions were violated, data were transformed (log 10 or square-root) and if variances were still heterogeneous, alpha was reduced to 0.01. Alpha was otherwise 0.05 in all tests. Tukey's Honest Significant Difference post hoc tests were used following significant ANOVA tests. All analyses were done in R version 3.5.0 (R Core Team 2017).

Effects of dead shells on benthic communities

Survey 4: Shell-epifauna survey

To assess the relationship between the presence of dead shells and the diversity of epifaunal communities, all epibenthic material was collected from three habitats (bare sediments, *Zostera muelleri* seagrass beds, and *Ulva* spp. seaweed beds), with and without presence of dead shells (presence ≥ 1 shell) using a 17 × 17 cm quadrat (bare n = 32, bare+shell n = 21, seagrass n = 6, seagrass+shell n = 3, seaweed n = 20, seaweed+shell n = 19). All epibenthic material, including surface-dwelling shells, seagrass leaves, seaweed, and macroinvertebrates were placed into a 1 mm mesh bag, and washed in the field to remove sediment. Not all six

types of habitats (3 habitats × 2 shell levels) could be collected from all sites (seagrass was present at only two of the sites). In the laboratory, invertebrates were identified and counted, and seaweed, dead shells, and seagrass leaf and root biomass were dried at 55°C for three days and weighed. ANOVA was used to test if dead bivalve shells and habitat type affected invertebrate densities (converted to m^{-2}) and taxonomic richness. Assumption tests and post hoc tests were conducted as described in Survey 1. In addition, non-metric multidimensional scaling (NMDS) and adonis tests (packages '*vegan'* and *'ecodist'*) were used to examine differences in invertebrate communities (using Bray-Curtis distance metrics) between habitats and shell presence; 5000 permutations were used in the adonis test. Significant results from the adonis test were followed by post-hoc pairwise-MANOVA tests (5000 permutations, Bonferroni correction, package *'RVAideMemoire'*). Finally, a similarity of percentages (SIMPER) analysis was used to determine the proportional contribution of individual taxa to variation among quadrats with and without shells.

Shell addition experiment: the effects of dead shells among latitudes, estuaries and habitats

A field experiment was set up in six estuaries (see 'study sites' Figure 5.1A) in summer (Oct-Feb) 2016/2017 to test for the effects of dead shells on (1) abundances and richness of epi- and in-fauna, (2) abundances and richness of seaweed recruits (attached to shells), (3) seagrass biomass, and (4) whether seagrass affects the retention of dead shells. In each estuary, six circular (15 cm diameter) plots were set up on bare sediment and 12 in adjacent seagrass beds. In half of the seagrass plots, the above-ground leaves were cut off with a pair of scissors ('Cut' treatment) while the other 6 plots were left intact ('Natural'). Large *Austrovenus* shells, previously dried and cleaned of sessile epibiota, were subsequently added to the centre (diameter ca. 9 cm) of half of all plots in a factorial design (n = 10-15 per plot). Shells were haphazardly inserted partially into the sediment, on top and around seagrass leaves, to mimic natural shell depositions (see Supplementary material for photos).

Treatment effects were evaluated by collecting circular cores (9 cm diameter × 10 cm depth) from each plot centre 2.5 months after the experiment was initiated. The cut-treatment tested how seagrass leaf loss affected invertebrates and whether shells impede recovery of seagrass leaves. Cores were washed in the field in 1 mm mesh-bags and placed in a -20°C freezer within 2 hours of being collected. To quantify shell retention, shells were collected (a) within the sediment core ('core samples') and (b) adjacent to the core ('outside cores'), by adding any remaining transplanted shells to a separate plastic bag (there were no background shells

to confuse with the transplanted shells). The amount of shells found in the core samples were converted to a percentage of the initial added number of shells (percent shell retention). In the laboratory, all cores samples were processed as described for the habitat survey. Furthermore, all shells from both the 'core samples' and 'outside cores' were examined in detail under a stereoscope at 8× magnification to identify and count faunal and algal colonizers attached to the shells (shells with abundant seaweed recruits, mainly *Ulva* spp., were subsampled by counting recruits within 1 cm^2 and then scaled per colonized area). Mobile and sessile organisms were counted, whereas encrusting bryozoans, snail egg masses, and the brown algae *Ralfsia* spp. were recorded as being present or absent. ANOVAs were used to test if: (a) invertebrate densities and richness were affected by shells, habitat, and latitude, (b) seagrass leaf and root biomass were affected by shells, habitat, and latitude (but only relevant for cut and natural seagrass plots), and (c) seaweed recruit density and richness, and shell retention were affected by habitat and latitude (but only relevant for the shell addition plots). Shell retention percentages were arcsine square-root transformed. Assumption tests and post hoc analyses for all tests were conducted as described for Survey 1. Non-metric multidimensional scaling, adonis-tests, and post-hoc pairwise-MANOVA tests were used to examine if invertebrate communities were affected by latitude, habitat and shells). Finally, a similarity of percentages (SIMPER) analysis was used to determine the proportional contribution of individual taxa to variation among plots with and without added shells.

Results

Distributions of dead shells in estuaries

Survey 1: Distribution of shells among estuaries and latitudes

Dead shells were found in all six sampled estuaries in the South Island (Figure 5.1-5.2, for analysis of seagrass and seaweed distributions see Chapter 2), although cover varied significantly between latitudinal regions and estuaries (arcsine square-root transformed; both $p < 0.001$, Table 5.1A). The northern region had significantly higher shell cover (22.1 ± 1.6%), followed by southern and central estuaries (8.1 ± 1.2 and 6.2 ± 0.7%, respectively, Table 5.1A, Figure 5.2). More specifically, Delaware Inlet in the North had the highest cover (30.6 ± 2.8%), followed by Portobello Bay in the South (15.8 ± 2.1%), whereas Papanui Inlet, also in the South, had the lowest cover (0.2 ± 0.2%, Figure 5.2).

Survey 2: Distribution of dead shells in silt and seagrass habitats

Shell cover varied significantly among habitats and sites (arcsine square-root transformed, $p < 0.001$, Table 5.1B). Seagrass habitats had higher cover of shells (22.6 ± 2.2%) than silty sites (9.8 ± 0.8%, Table 5.1B, Figure 5.3). Tern Street had the highest cover (30.8 ± 2.6%), followed by the Causeway (12.5 ± 1.1%), Oxidation Ponds (6.6 ± 1.2%), and Plover Street (5.6 ± 0.4%, Table 5.1B, Figure 5.3).

Survey 3: Temporal distribution of dead shells

The cover of dead shells did not vary between seasons ($p = 0.109$) but varied significantly between sites ($p < 0.001$, Table 5.1C, Figure 5.4A, B), with greater cover at Tern Street (9.4 ± 0.4%) than at Plover Street 5.6 ± 0.3%).

Effects of dead shells on benthic communities

Survey 4: Shell-epifauna survey

Invertebrate densities and taxonomic richness (log 10 +1 transformed) were significantly affected by shells ($p < 0.001$) with significant variation among habitats (Shell × Habitat, $p < 0.001$, Table 5.2, Figure 5.5A). Invertebrate densities were generally much higher in presence of shells (2080.9 ± 297.1 m^{-2}) than without (429.5 ± 83.5 m^{-2}) and were highest in the *Ulva* habitat (1560.6 ± 312.8 m^{-2}) followed by seagrass (1138.0 ± 163.7 m^{-2}) and bare sediments (816.7 ± 181.2 m^{-2}, Table 5.2A, Figure 5.5A). Similarly, richness was also higher in presence of shells (5.1 ± 0.3 $quadrat^{-1}$) than without (2.7 ± 0.2 $quadrat^{-1}$, Table 5.2B, Figure 5.5B) and higher in seagrass habitat (4.8 ± 0.5 $quadrat^{-1}$), followed by *Ulva* (4.3 ± 0.3 $quadrat^{-1}$), and bare sediments (3.2 ± 0.3 $quadrat^{-1}$, Table 5.2B, Figure 5.5B). The NMDS plot (2 dimensions, stress = 0.158) also showed different invertebrate communities between samples with and without shells (adonis test, $R^2 = 0.17$ $p < 0.001$), although effects varied among habitats (Shell × Habitat, $R^2 = 0.04$, $p < 0.001$, Table 5.2C, Figure 5.6). Follow up post hoc tests showed that bare sediment samples were different from all samples with biogenic habitat formers, '+Shell' samples were similar to Seagrass samples, and the *Ulva*+Shell and Bare+Shell habitats were different from *Ulva* samples (Figure 5.6). The SIMPER analysis revealed an 80% total difference in communities where dead shells were present or absent, with four taxa; *Notoacmea* spp., *Micrelenchus huttonii*, *Diloma nigerrimum* and juvenile crabs contributing to 82% of that difference (Table 5.3).

Shell addition experiment: the effects of dead shells among latitudes, estuaries, and habitats

Effects on biodiversity

Invertebrate densities (log 10 +1 transformed) and taxonomic richness were significantly affected by latitude ($p < 0.003$), the presence of shells ($p < 0.001$), and habitats ($p < 0.007$), but there were no significant interactions. Invertebrate densities were highest in the central region (5418.5 ± 1284.5 m^{-2}), followed by the northern region (3820.0 ± 645.8 m^{-2}), and lowest in the southern region (2300.1 ± 463.9 m^{-2}). By comparison, richness was highest in the northern region (6.4 ± 0.6 $quadrat^{-1}$), intermediate in the central region (5.1 ± 0.5 $quadrat^{-1}$), and lowest in the southern region (4.2 ± 0.5 $quadrat^{-1}$). Densities were almost 5× higher in the presence of shells (6604.9 ± 946.9 m^{-2}) than without shells (1329.8 ± 168.1 m^{-2}) and were higher in seagrass habitats (Natural: 4479.7 ± 894.7 m^{-2}, Cut: 3998.9 ± 713.1 m^{-2}) than in bare sediments (3203.3 ± 1246.2 m^{-2}) (Table 5.4A, Figure 5.7A). Invertebrate richness was 2× higher when shells were present (7.4 ± 0.4 $quadrat^{-1}$) than when shells were absent (3.3 ± 0.3 $quadrat^{-1}$), and, again, higher in seagrass habitats (Natural: 6.1 ± 0.5 $quadrat^{-1}$, Cut: 5.4 ± 0.5 $quadrat^{-1}$) than in bare sediments (4.1 ± 0.6 $quadrat^{-1}$) (Table 5.4B, Figure 5.7B). NMDS plots from the 6 estuaries (2 dimensions, stress = 0.211) showed that benthic invertebrate communities differed between samples with and without shells (adonis test, $R^2 = 0.09$, $p < 0.001$). The adonis test also showed that community structure varied among sampled region and habitats ($R^2 = 0.05$, $p = 0.001$, Table 5.4C, Figure 5.8), as well as region and shell presence ($R^2 = 0.04$, $p < 0.001$, Table 5.4C). Post hoc tests revealed that cut and natural seagrass samples were similar, but differed from bare sediments, and that all shell-addition treatments were different from samples without shells. SIMPER analysis revealed an 87% total difference in communities where dead shells were either absent or present. Eight taxa contributed 77% of the difference between communities with *Notoacmea* spp., *Micrelenchus huttonii*, snail egg sacs, and unidentified barnacles contributing > 10% each of the differences between communities (Table 5.5).

Effects on seaweed recruits

The density and richness of seaweed recruits on shells (log 10+1 transformed) differed among habitats ($p < 0.001$ for both tests) and was similar among geographic regions (Region × Habitat, $p = 0.464$ and 0.171, respectively, Table 5.5D-E). Highest densities were found in the Natural+Shell treatment (37217.5 ± 11984.8 m^{-2}), followed by Cut+Shell (33672.2 ±

8856.3 m^{-2}), and lowest in Bare+Shell (8959.4 ± 5195.1 m^{-2}, Figure 5.7C), whereas highest richness was found in the Cut+Shell treatment (1.2 ± 0.1 $quadrat^{-1}$), followed by Natural+Shell (1.0 ± 0.1 $quadrat^{-1}$), and lowest in the Bare+Shell (0.5 ± 0.1 $quadrat^{-1}$, Figure 5.7D).

Reciprocal effects of shells and seagrass

Seagrass leaf biomass (log 10+1 transformed) was affected by presence of shells ($p = 0.003$), habitat ($p = 0.004$), and latitudinal region ($p = 0.002$), where effects of the latter varied between habitats (Region × Habitat, $p = 0.048$) (Table 5.6A). Seagrass leaf biomass was greater where shells were absent (57.8 ± 6.7 $gDW \cdot m^{-}2$) compared to when they were added (33.6 ± 6.6 $gDW \cdot m^{-2}$). Leaf biomass was also greater where seagrass was unmanipulated compared to where it had been cut (58.3 ± 8.0 $gDW \cdot m^{-2}$ vs 33.1 ± 4.9 $gDW \cdot m^{-2}$, respectively). Across latitudes, seagrass leaf biomass was greatest in the southern region (66.2 ± 9.3 $gDW \cdot m^{-2}$) followed by the northern region (39.5 ± 8.9 $gDW \cdot m^{-2}$) with the lowest biomass found in the central region (31.4 ± 5.2 $gDW \cdot m^{-2}$) (Figure 5.9A). Root biomass was only affected by latitudinal regions ($p < 0.001$, Table 5.6B, Figure 5.9B) with highest biomass in the south (478.3 ± 31.3 $gDW \cdot m^{-2}$), followed by the north (104.4 ± 8.9 $gDW \cdot m^{-2}$), and with the lowest biomass in the central region (71.6 ± 6.3 $gDW \cdot m^{-2}$).

Finally, retention of dead shells was affected by latitudinal region ($p = 0.002$) where effects varied between habitat (Region × Habitat, $p = 0.026$, Table 5.6C). The central region had highest retention (37.7 ± 4.7%), followed by the southern region (31.1 ± 3.6%), and with lowest retention in the northern region (15.8 ± 3.2%). Tukey's post hoc tests showed that the central Bare+Shell treatment retained more shells than the northern Cut+Shell and Natural+Shell treatments (Figure 5.9C; no other comparisons were significant).

Discussion

The results presented in this chapter show that bivalves can have leave a significant legacy for biodiversity in estuarine systems after their death. Their shells, empty of flesh, were a common habitat in all surveyed estuaries where their presence increased the abundance and diversity of invertebrate and algal communities across habitats and latitudes. These results support the notion that dead shell deposits can become small-scale 'hotspots' of biodiversity that are comparable to other biogenic habitats such as seagrasses and seaweeds when they

enhance a bare mudflat (Orth et al. 1984, Cummings et al. 1998, Bially and Macisaac 2000, Boström and Bonsdorff 2000, Thrush et al. 2001, Orlova and Panov 2004, Boström et al. 2006, Wasson 2010, Thomsen et al. 2016). When dead shells were found among or associated with foundation species such as seagrass, they also increased epifaunal biodiversity of those habitats, suggesting that dead shells can play a role in estuarine facilitation cascades (Altieri et al. 2007, Thomsen et al. 2016).

Distributions of dead shells in estuaries

Dead shells were found in all latitudes and estuaries surveyed in this study. In the Avon-Heathcote Estuary (central region of the South Island), dead shells were found in all sites, habitats, and seasons. The dead shells found were mainly from the culturally and economically important little-necked clam, *Austrovenus stutchburyi* (Williams et al. 2006, Smith 2013, Kainamu-Murchie et al. 2018) although other shells such as *Macomona liliana* and *Paphies australis* were also found. Other studies have found dead shells to be common on benthic sediments. For example, in Manukau Harbour in the North Island of New Zealand, a dredge survey of 45 stations found that almost half had dead bivalve shells as a large component of the benthic habitat (Grange 1979). On the edge of the Hikurangi Margin tectonic plate near New Zealand, bivalve shells were found in 75% of all deep-sea methane seep sediments (with some areas "paved with clam shells"), demonstrating that these shell deposits had existed for long periods from the extent of the shell- deposition found (Greinert et al. 2010). Indeed, dead bivalve shells are common in sedimentary systems around the world, including in Europe (Pinkster and Broodbakker 1980, Murray 1983, Ilarri et al. 2014), North America (Surge et al. 2003, Powell et al. 2006, Gagné et al. 2008), and Australia (Chalmer et al. 1976, Summerhayes et al. 2009).

Effects of dead shells on benthic communities

Dead shells altered community structure and increased abundances and richness of invertebrates across latitudes, estuaries, sites, habitats, and seasons. Other studies that examined effects of dead shells (mainly oysters or zebra mussels) found similar facilitation of invertebrates (Dauer et al. 1982, Ricciardi et al. 1997, Eggleston et al. 1999, Tolley and Volety 2005). It is likely that dead shells increased the quantity of hard substrata, that is usually a limiting factor for epifaunal biodiversity in estuaries. It is also likely that the

presence of dead shells modifies bed-flow dynamics (Commito et al. 2014), provides refuge from predation (Bódis et al. 2014), or facilitates food supply such as biofilm development on the shell-surfaces (Bonar et al. 1990, Tamburri et al. 1992). Importantly, dead shells increased diversity when co-occurring with other habitat-formers, like seagrass and seaweed, suggesting that combinations of different types of substrata facilitate invertebrates through the provision and modification of habitat (Ricciardi et al. 1997, Posey et al. 1999, Healey and Hovel 2004, Boström et al. 2006, Mills and Berkenbusch 2009). For example, dead pen shells (*Atrina rigida*) embedded in seagrass beds increased densities and richness of invertebrates compared to seagrass alone with ca. 65% of sampled invertebrate species only being found on the shells (Munguia 2007). These results demonstrate that legacy effects may be common drivers of facilitation cascades to modify or control biodiversity (Altieri et al. 2007, Thomsen et al. 2010a, Angelini and Silliman 2014, Thomsen et al. 2018b).

Dead shells increased the number and diversity of seaweed recruits by providing a suitable surface for their recruitment, supporting other studies that have shown facilitation of algae by bivalves (Kidwell and Jablonski 1983, Gutiérrez et al. 2003, Thomsen 2004, Gribben and Wright 2006). The lowest seaweed recruitment was on shells in bare sediments, with the greatest recruit densities and richness in plots with seagrass. Perhaps these habitat-associated differences occur because bottom current velocities are slower in seagrass beds, promoting the settlement of recruits (Fonseca et al. 1982, Peterson et al. 1984, Butman 1986), or because sediment scouring, and smothering are more prevalent in bare sediments. On rocky shores, Umar et al. (1998) found that sediments smothered and inhibited recruits of *Sargassum microphylla*. Indeed, even a small amount of added sediment (10 $mg \cdot cm^{-2}$) prevented attachment of *Macrocystis pyrifera* through abrasive scouring (Devinny and Volse 1978) and light dusting of sediment reduced survival of attached recruits of *Durvillaea antarctica* by 71% and *Hormosira banksii* by 34% in laboratory experiments, while complete coverage of sediment prevented any form of attachment (Schiel et al. 2006) Indeed, some of the experimental shells were covered by sediment at the end of in the shell-addition experiment.

Shells and seagrass reciprocal effects

Dead shells had negative effects on seagrass leaf biomass (but not root/rhizome biomass). Regrowth of seagrass leaves was smaller in the presence of shells. This reduction in leaf regrowth may be caused by low light levels beneath the shells (Brun et al. 2003b, Carroll et al. 2008) or through abrasion, smothering, and competition for space (Holmer et al. 2005). It

has previously been shown that dead oyster shells (20% cover of *Crassostrea gigas*) reduced seagrass density by >60%, also in the presence of added nutrients (Wagner et al. 2012). However, other studies have shown that adding low (15 m^{-2}) to medium (75 m^{-2}) densities of live oysters (*Crassostrea virginica*) facilitated growth, and even large densities (150 m^{-2}) had no effects, probably due to the addition of porewater nutrients to the sediments (Booth and Heck Jr. 2009). In contrast to expectations, I found that the retention of dead shells was not enhanced in seagrass beds, even though hydrodynamic drag forces are lowered by some seagrasses (Fonseca et al. 1982, Peterson et al. 1984, Fonseca and Cahalan 1992). Perhaps shells in the seagrass beds experience whiplash from seagrass leaves, which may move the shells in the bed during storms. In fact, movement of seagrass leaves has been shown to reduce epiphyte biomass (Borowitzka et al. 2006, Lavery et al. 2007), remove grazers (Schanz et al. 2002), and increase recruitment of mussels due to the sweeping motions of the leaves through the water column (Grizzle et al. 1996). Finally, the lack of difference in retention between habitats may also be due to the relatively short timeframe of the experiment and the lack of any major storms occurring over the experimental period.

The value of dead shells

In addition to supporting important ecosystem functions (Dauer et al. 1982), dead shells are also indirectly valuable to humans. For example, oyster larvae are chemically attracted to settle on conspecific dead shells, and thereby facilitate formation and maintenance of commercially important oyster beds (Abbe 1988, Turner et al. 1994). Shells also add other ecosystem services: decomposition of bivalve shells is important for carbonate cycling of aquatic systems and allows new generations of shell-producing organisms to grow (Waldbusser et al. 2011, Waldbusser et al. 2013). In addition, shells alter sediment boundary layer characteristics (Gutiérrez et al. 2003) and can stabilize sediments to reduce erosion and increase water clarity (Hewitt et al. 2005).

Bivalves have been a part of human diets for millennia as evidenced by middens on land (Erlandson 2001, Gardner 2004, Helama and Hood 2011). The practice of disposing of the shells of marine organisms on land continues today, and shells from consumed bivalves are rarely returned to the aquatic systems. For example, for every kg of oysters produced, 370-700g of shell waste is produced, and in China, 10 million tons of shell waste are added annually to landfills (Yao et al. 2014). Little research has addressed this shell-transfer from ocean-to-land but is has been suggested that returning commercially harvested bivalve shells

to the aquatic environment on large scales potentially could mitigate some effects of ocean acidification and assist in bivalve reef restoration (Green et al. 2009, NIWA 2015, Clements and Chopin 2016).

Conclusions

It is well-established that many living bivalves are foundation species. Here I showed that shells from a dead bivalve were abundant in estuaries in New Zealand, and that these shells increased abundances and diversity of benthic invertebrates, enhanced seaweed recruitment, but had negative effects on seagrass leaves. I suggest that the foundation species concept should include legacy effects, for example from dead tree trunks and shell-producing organisms, and that dead shells are a fundamental and integrated component of estuarine habitats and therefore should be included in future research and conservation of these important systems.

Tables

Table 5.1 ANOVA table for of percent cover of surface-dwelling dead shells (Arcsine square-root transformed) from (A) a latitudinal survey of 6 estuaries from 3 regions, (B) a spatial 2014 survey in the Avon-Heathcote Estuary in 2 habitats (silty sites vs. seagrass sites, 4 sites) and 2 sites, and (C) a two-year seasonal survey from the Avon-Heathcote Estuary (summer vs. winter, 2 sites). Alpha was reduced to 0.01 in all tests because variance homogeneity could not be confirmed. Significant effects are in bold.

Method	Test Factor	Df	SS	F-value	p
(A) Latitudinal Survey	**Region**	**2**	**7.728**	**92.81**	**<0.001**
	Estuary	**3**	**7.317**	**58.59**	**<0.001**
	Residuals	544	22.648		
(B) 2014 Survey	**Habitat**	**1**	**2.344**	**73.54**	**<0.001**
	Site	**2**	**3.297**	**51.71**	**<0.001**
	Residuals	244	7.778		
(C) 2014-2016 Survey	Season	1	0.049	2.575	0.109
	Site	**1**	**1.187**	**62.606**	**<0.001**
	Season×Site	1	0.013	0.68	0.410
	Residuals	989	18.757		

Table 5.2 ANOVA table for invertebrate (A) density (m^{-2}, log 10+1 transformed), (B) taxonomic richness ($quadrat^{-1}$, log 10+1 transformed), and (C) multivariate community structure from a 2014 spatial survey in three habitats around the Avon-Heathcote Estuary. Shell = presence-absence of shells; Habitat = bare (unvegetated) sediments, the seagrass *Zostera muelleri*, and the seaweed *Ulva* spp. Significant effects are in bold.

Measure	Test Factor	Df	SS	F-value	p
(A) Density	**Shell**	**1**	**17.11**	**162.73**	**<0.001**
	Habitat	**2**	**4.944**	**23.51**	**<0.001**
	Shell×Habitat	**2**	**2.158**	**10.26**	**<0.001**
	Residuals	95	9.989		
(B) Richness	**Shell**	**1**	**1.3103**	**69.78**	**<0.001**
	Habitat	**2**	**0.4395**	**11.7**	**<0.001**
	Shell×Habitat	**2**	**0.3984**	**10.61**	**<0.001**
	Residuals	95	1.7839		
(C) Community Structure	**Shell**	**1**	**6.836**	**31.627**	**<0.001**
	Habitat	**2**	**3.513**	**8.127**	**<0.001**
	Shell×Habitat	**2**	**1.438**	**3.326**	**<0.001**
	Residuals	128	27.667		

Table 5.3 Dissimilarity table (SIMPER test) of invertebrate communities between quadrats where shells were either present or absent in a survey in the Avon-Heathcote Estuary. Listed are taxa that explain 82.2% of the dissimilarity between the two communities, with each organism's contribution, as well as mean abundances ± SE per quadrat. The total overall dissimilarity between the shell-present and shell-absent communities was 80%.

Species	+Shell Abundance	-Shell Abundance	Dissimilarity Contribution (%)	Cumulative Dissimilarity (%)
Notoacmea spp.	27.6 ± 4.1	1.6 ± 0.3	41.04	41.04
Micrelenchus huttonii	14.1 ± 2.0	4.5 ± 1.0	25.03	66.07
Diloma nigerrimum	5.6 ± 0.7	2.0 ± 0.2	9.73	75.8
Juvenile crabs (unID)	1.9 ± 0.5	2.7 ± 1.5	6.36	82.16

Table 5.4 ANOVA table for invertebrate (A) density (m^{-2}, log 10+1 transformed), (B) taxonomic richness, (C) multivariate community structure, and on seaweed (D) densities (m^{-2}, log 10+1 transformed)) and (E) richness (log 10+1 transformed) recruited to out-transplanted shells, from an experiment conducted in six estuaries from three regions (North, Central, South) on the South Island of New Zealand. Shell = presence/absence of shells (adding 10-15 shells per plot). Habitat = bare sediments, seagrass habitat with leaves cut, and undisturbed natural seagrass. Note that seaweed responses were only relevant to test in shell addition treatments (and therefore excluded the Shell-test factor). Significant effects are in bold.

Measure	Test Factor	Df	SS	F-value	p
(A) Faunal Density	**Region**	**2**	**3.208**	**6.646**	**0.002**
	Shell	**1**	**12.832**	**53.17**	**<0.001**
	Habitat	**2**	**2.624**	**5.436**	**0.006**
	Region×Shell	2	0.494	1.023	0.364
	Region×Habitat	4	1.278	1.324	0.268
	Shell×Habitat	2	0.113	0.235	0.791
	Region×Shell×Habitat	4	0.912	0.945	0.442
	Residuals	81	19.549		
(B) Faunal Richness	**Region**	**2**	**72.6**	**7.995**	**<0.001**
	Shell	**1**	**396.1**	**87.23**	**<0.001**
	Habitat	**2**	**54.2**	**5.971**	**0.004**
	Region×Shell	2	3	0.333	0.718
	Region×Habitat	4	26.5	1.459	0.222
	Shell×Habitat	2	0.8	0.087	0.917
	Region×Shell×Habitat	4	22	1.214	0.311
	Residuals	81	367.8		
(C) Community Structure	**Region**	**3**	**5.545**	**7.312**	**<0.001**
	Shell	**1**	**3.192**	**12.628**	**<0.001**
	Habitat	**2**	**1.165**	**2.304**	**0.001**
	Region×Shell	**2**	**1.344**	**2.659**	**<0.001**
	Region×Habitat	**4**	**1.872**	**1.852**	**0.001**
	Shell×Habitat	**2**	**1.003**	**1.984**	**0.005**
	Region×Shell×Habitat	4	1.062	1.050	0.370
	Residuals	80	20.224		
(D) Seaweed Recruit Density	Region	2	1.29	0.304	0.74
	Habitat	**2**	**39.63**	**9.301**	**<0.001**
	Region×Habitat	4	7.81	0.917	0.464
	Residuals	40	85.22		
(E) Seaweed Recruit Richness	Region	2	0.0357	1.321	0.278
	Habitat	**2**	**0.1902**	**7.041**	**0.002**
	Region×Habitat	4	0.0914	1.692	0.171
	Residuals	40	0.5404		

Table 5.5 Dissimilarity table (SIMPER test) of invertebrate communities between plots with or without added shells in a latitudinal experiment in six estuaries. Listed are taxa that explain 77.6% of the dissimilarity between the two communities, with each organism's contribution, as well as mean abundance ± SE per core listed. The total overall dissimilarity between the shell-present and shell-absent communities was 87%.

Species	+Shell Abundance	-Shell Abundance	Dissimilarity Contribution (%)	Cumulative Dissimilarity (%)
Micrelenchus huttonii	5.4 ± 1.2	2.4 ± 0.7	15.01	15.01
Notoacmea spp.	8.1 ± 1.7	0.2 ± 0.1	14.37	29.38
Snail Egg sac	5.7 ± 1.4	0.0 ± 0.0	13.20	42.58
Barnacle (unID)	11.8 ± 4.1	0.0 ± 0.0	12.07	54.65
Small *Austrovenus stutchburyi*	1.6 ± 0.3	1.9 ± 0.3	7.83	62.48
Diloma nigerrimum	2.2 ± 0.4	0.2 ± 0.1	5.77	68.25
Zeacumantus subcarinatus	1.3 ± 0.3	0.4 ± 0.1	4.87	73.12
Nucula spp.	1.2 ± 0.4	0.8 ± 0.2	4.46	77.58

Table 5.6 ANOVA table for (A) seagrass leaf biomass, (B) seagrass root biomass (log 10+1 transformed), and (C) shell retention (arcsine square-root transformed), from an experiment conducted in six estuaries from three regions (North, Central, South) on the South Island of New Zealand. Shell = presence-absence of shells (adding 10-15 shells per plot). Habitat = bare sediments, seagrass habitat with leaves cut, and undisturbed natural seagrass. Note that seagrass responses were only relevant to test in the seagrass habitat (and therefore excluded the bare mud habitat), whereas the shell retention response only was relevant to test in the shell addition treatment (and therefore excluded the Shell-test factor). Significant effects are in bold.

Measure	Test Factor	Df	SS	F-value	p
(A) Seagrass Leaf Biomass	**Region**	**2**	**15952**	**6.683**	**0.002**
	Shell	**1**	**10574**	**8.86**	**0.004**
	Habitat	**1**	**11492**	**9.629**	**0.003**
	Region×Shell	2	3712	1.555	0.22
	Region×Habitat	**2**	**7640**	**3.201**	**0.048**
	Shell×Habitat	1	362	0.303	0.584
	Region×Shell×Habitat	2	1067	0.447	0.642
	Residuals	60	71607		
(B) Seagrass Root Biomass	**Region**	**2**	**9.388**	**131.035**	**<0.001**
	Shell	1	0.079	2.208	0.143
	Habitat	1	0.045	1.267	0.265
	Region×Shell	2	0.024	0.331	0.72
	Region×Habitat	2	0.071	0.986	0.379
	Shell×Habitat	1	0.031	0.862	0.357
	Region×Shell×Habitat	2	0.024	0.329	0.721
	Residuals	60	2.149		
(C) Shell Retention	**Region**	**2**	**0.6718**	**7.078**	**0.002**
	Habitat	2	0.0935	0.985	0.382
	Region×Habitat	**4**	**0.5869**	**3.091**	**0.026**
	Residuals	42	1.9934		

Figures

Figure 5.1 (A) Locations of six estuaries on the South Island of New Zealand sampled in a large scale latitudinal survey and where shell-addition experiments were carried out. **(**B) Locations of sites surveyed in the Avon-Heathcote Estuary from 2014 to 2016. Plover and Tern streets are seagrass dominated sites, whereas the Causeway and Oxidation pond sites are dominated by silty unvegetated sediments. The Heathcote River flows into the estuary in the southwest corner, while the Avon River flows from the northern side. The estuary opens into the Pacific Ocean in the southeast corner.

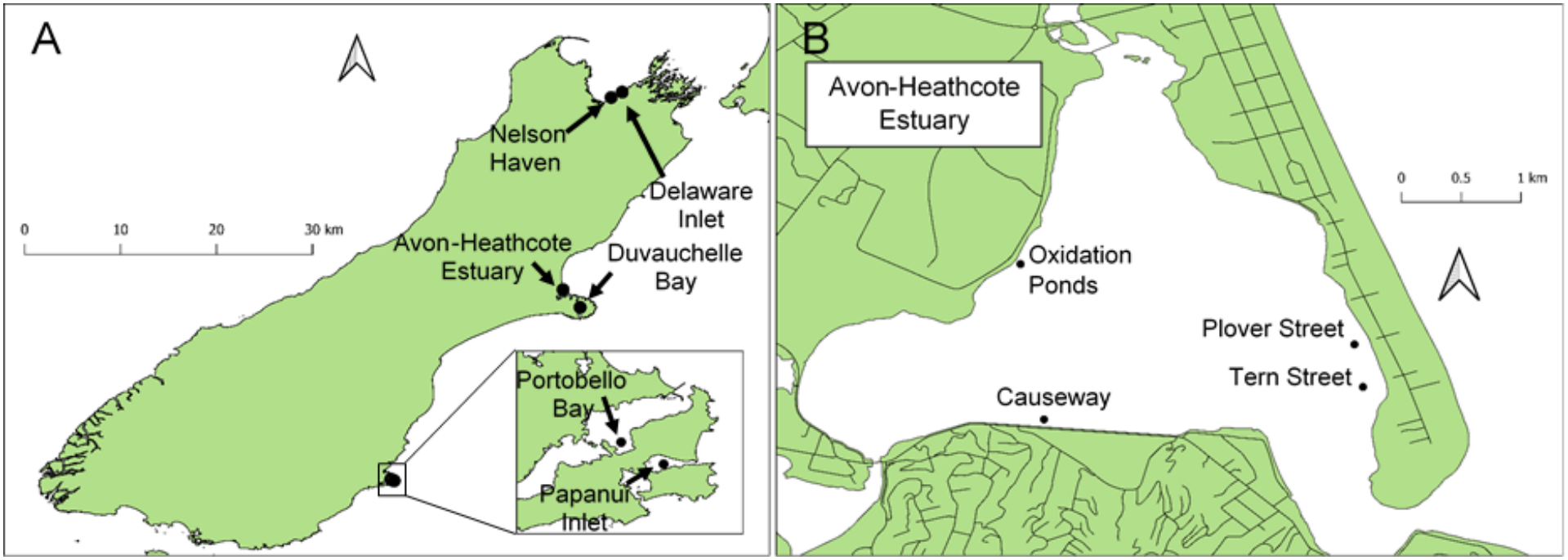


Figure 5.2 Percent cover (+SE) of dead shells, seagrass, seaweed and bare sediments in six estuaries across three latitudinal regions on the South Island, New Zealand.

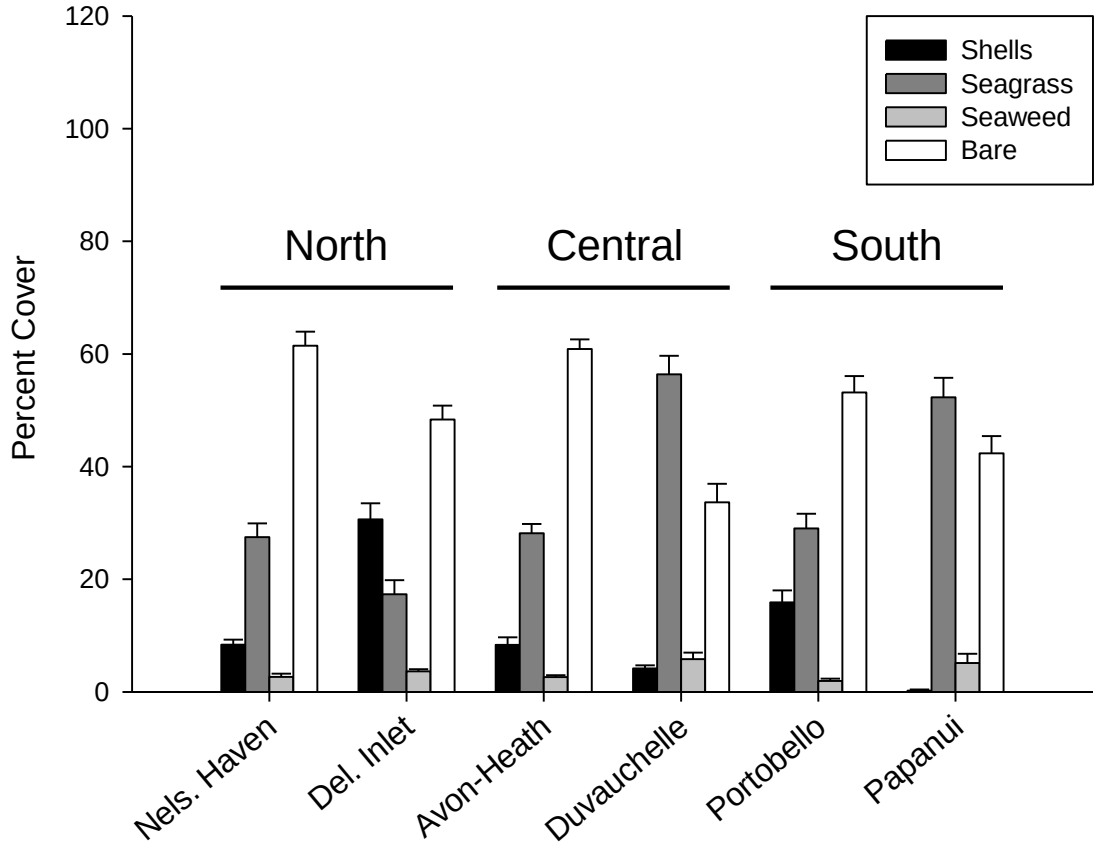


Figure 5.3 Percent cover (+SE) of dead shells, seagrass, seaweed and bare sediments in silty (no seagrass, Oxidation Ponds, Causeway) and seagrass dominated (Plover and Tern Street) habitats in the Avon-Heathcote Estuary in summer 2014.

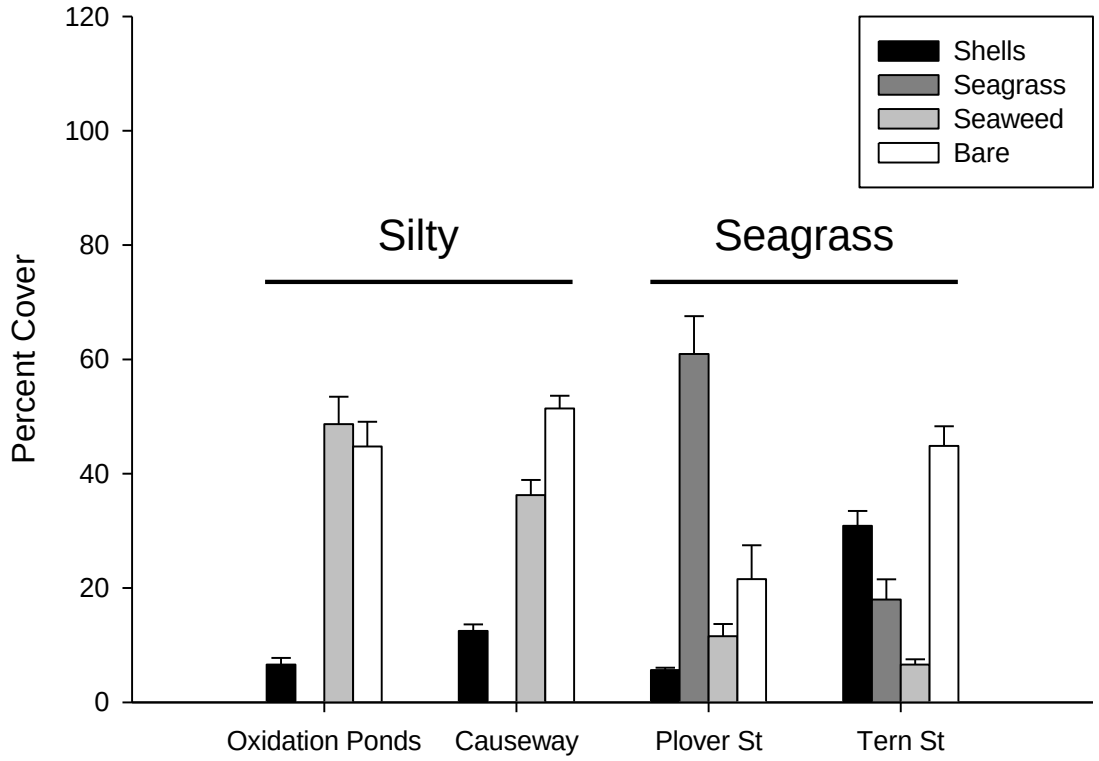


Figure 5.4 Percent cover (+ SE) of dead surface dwelling shells, seagrass, seaweed and bare sediment at (A) Plover Street and (B) Tern Street, in early/late summer (December-March) and winter (May-August) from 2014 to 2016 in the Avon-Heathcote Estuary (data for August 2015 (both sites) and November 2015 (Plover only) were lost).

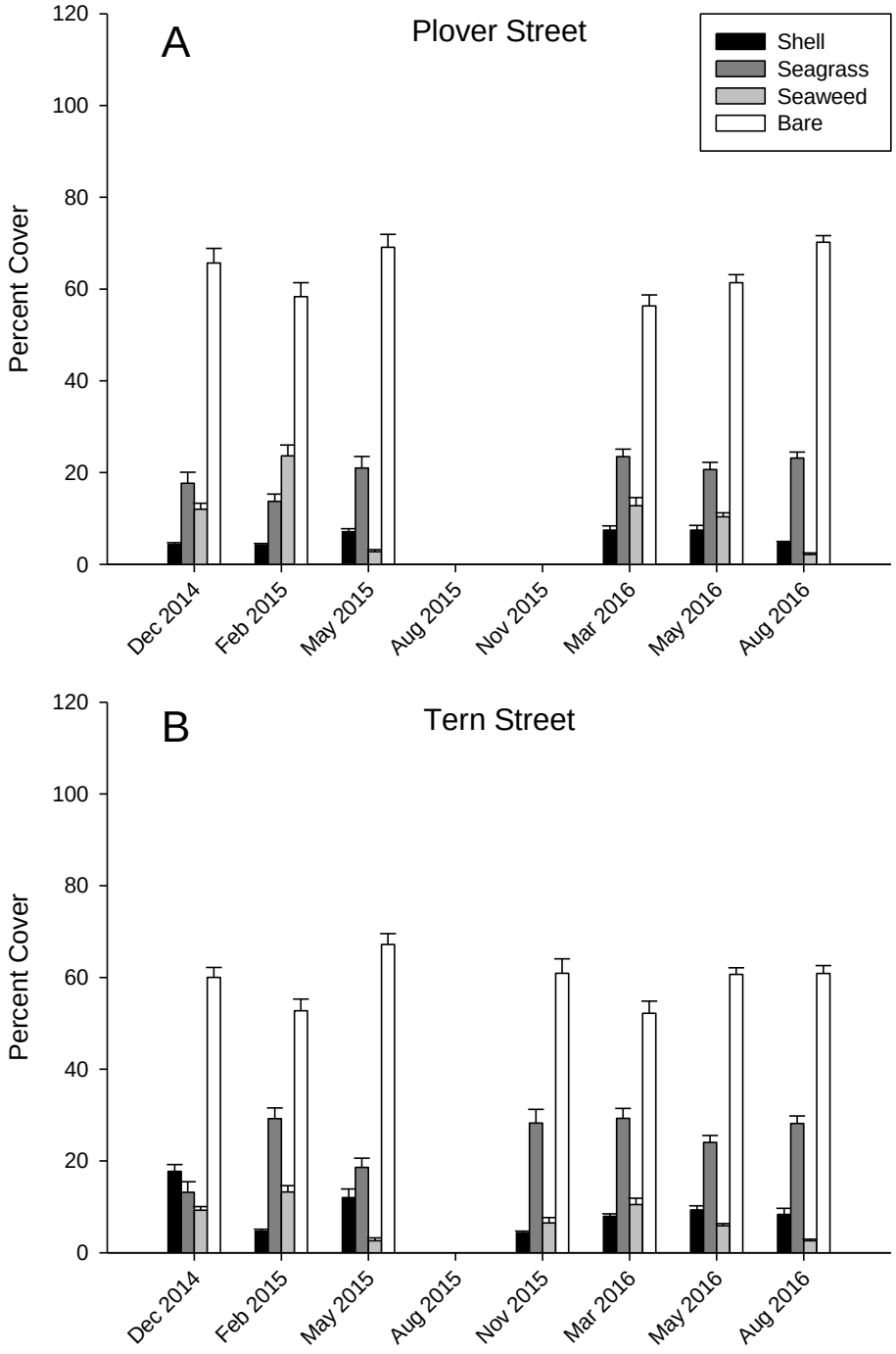


Figure 5.5 Epibenthic invertebrate (A) densities and (B) taxonomic richness (+SE) in summer 2014 from three habitats with and without presence of dead shells (collected from 4 sites in the Avon-Heathcote Estuary). Bare = unvegetated sediments, Shell = dead shells on the sediment, Seagrass = *Zostera muelleri*, and Ulva = the green seaweeds *Ulva* spp., quadrat size = 17 cm × 17 cm (0.0289 m^2), black bars = presence of dead shells.

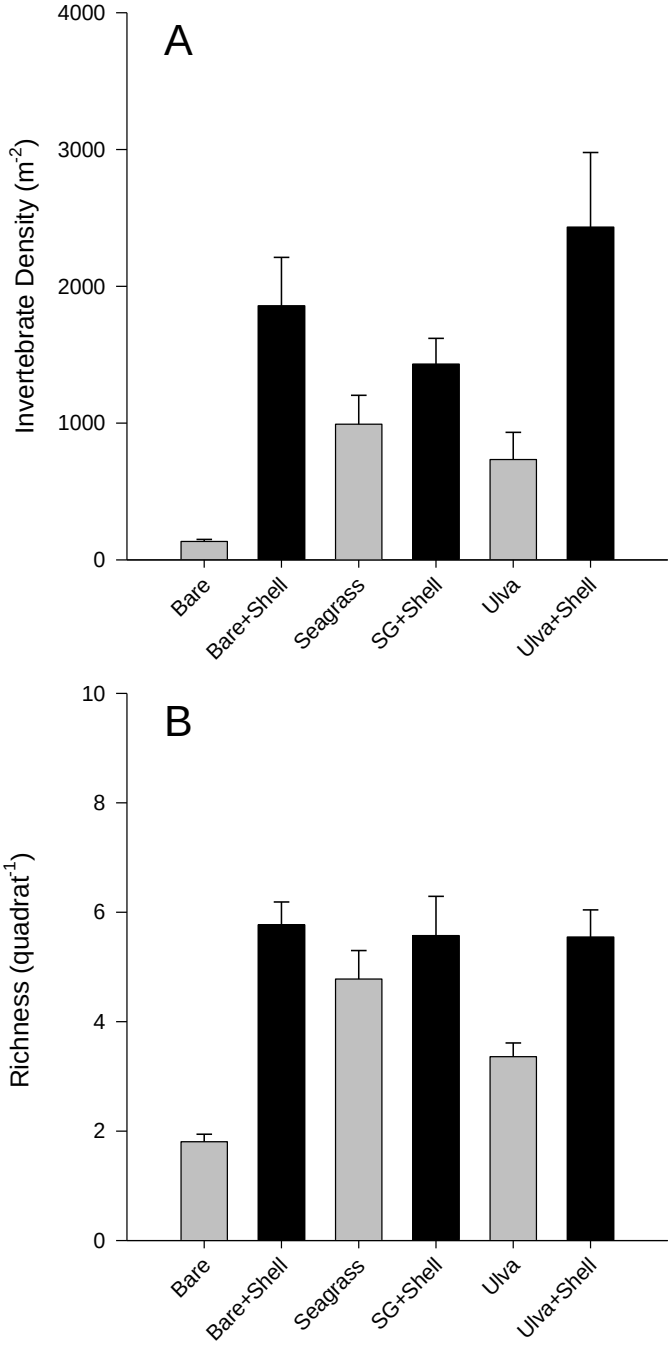


Figure 5.6 Non-metric multidimensional scaling (NMDS) plot of epibenthic invertebrate community structures (samples from summer 2014) associated with three habitats with (black) and without (white) dead shells. Bare = unvegetated sediments, Shell = dead shells on the sediment, Seagrass = *Zostera muelleri*, and Ulva = the green seaweeds *Ulva* spp., quadrat size = 17 cm × 17 cm (0.0289 m^2).

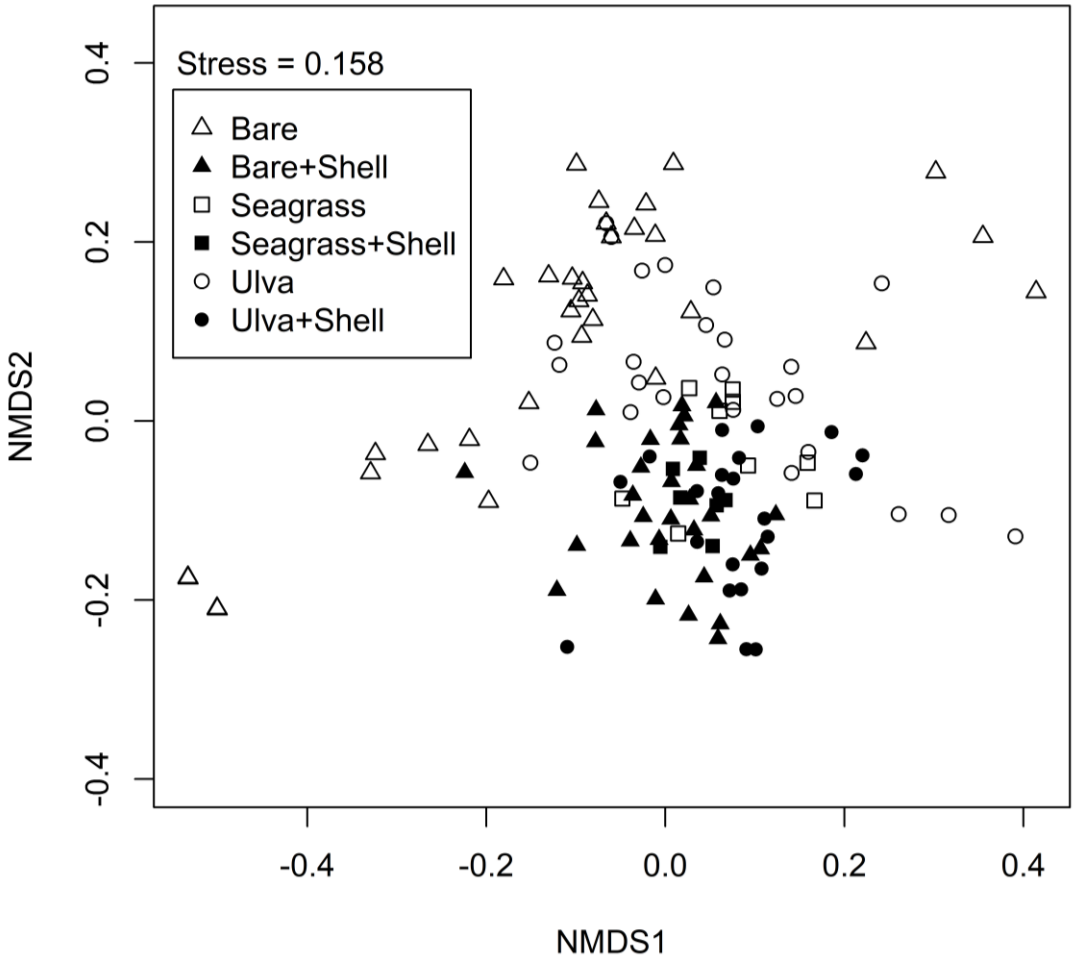


Figure 5.7 Invertebrate (A) density (m^{-2}) and (B) taxonomic richness ($core^{-1}$) and recruiting seaweed (C) density (m^{-2}) and (D) richness ($core^{-1}$, = 9 cm circular diameter) recruited onto out-transplanted shells, from an experiment conducted in six estuaries from three regions (North, Central, South) on the South Island of New Zealand. Shell = presence-absence of shells (adding 10-15 shells per plot). Habitat = bare sediments, seagrass habitat with leaves cut (Cut), and undisturbed natural (Nat) seagrass, black = presence of dead shells. Note that seaweed responses were only relevant to test in the shell addition treatment (and therefore excluded the Shell-test factor).

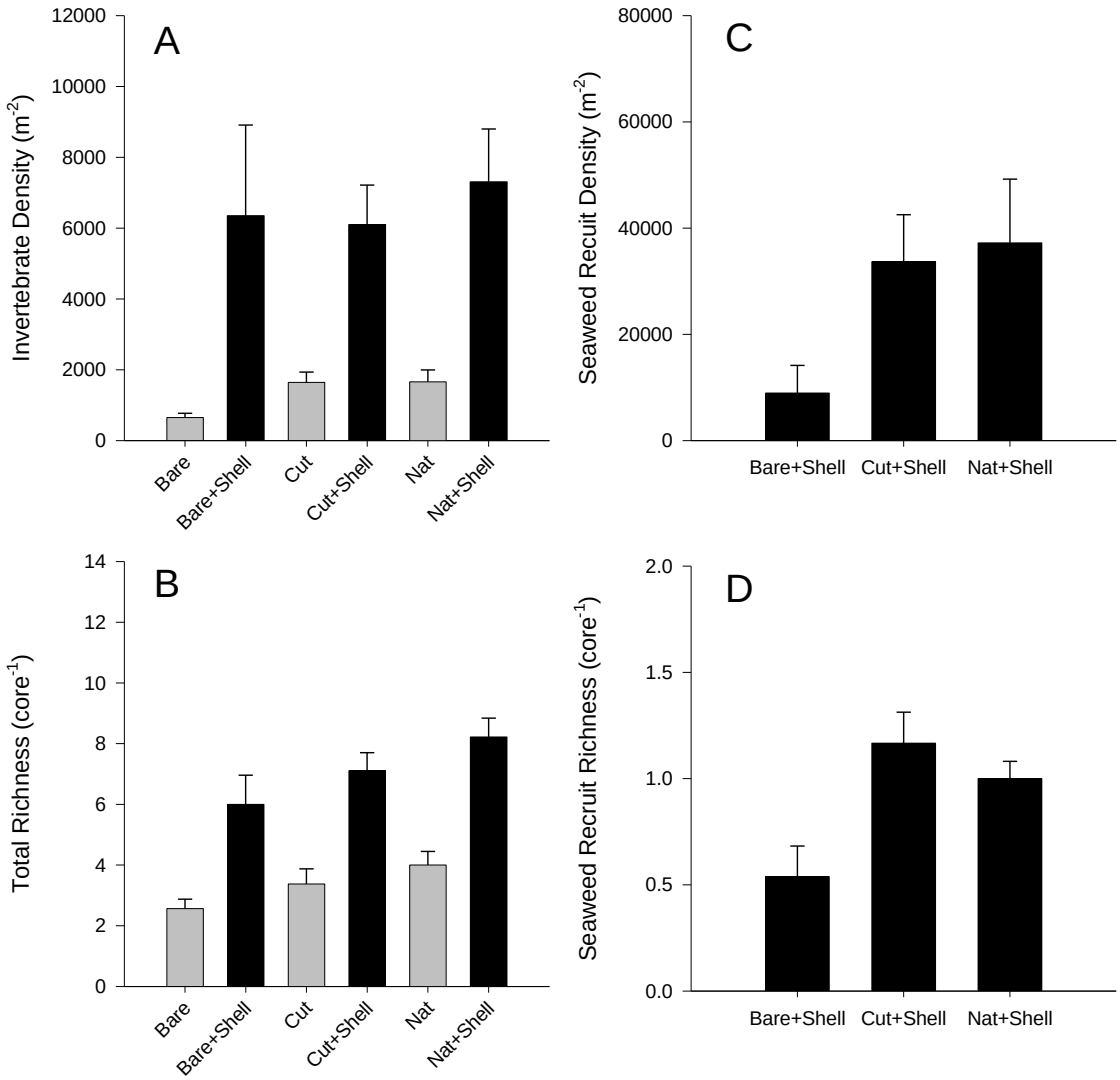


Figure 5.8 A non-metric multidimensional scaling (NMDS) plot of benthic invertebrate community structure (samples from summer 2016) from an experiment conducted in six estuaries from three regions (North, Central, South) on the South Island of New Zealand. Shell = presence-absence of shells (adding 10-15 shells per plot). Habitat = bare sediments, seagrass habitat with leaves cut (Cut), and undisturbed natural (Nat) seagrass, black = presence of dead shells.

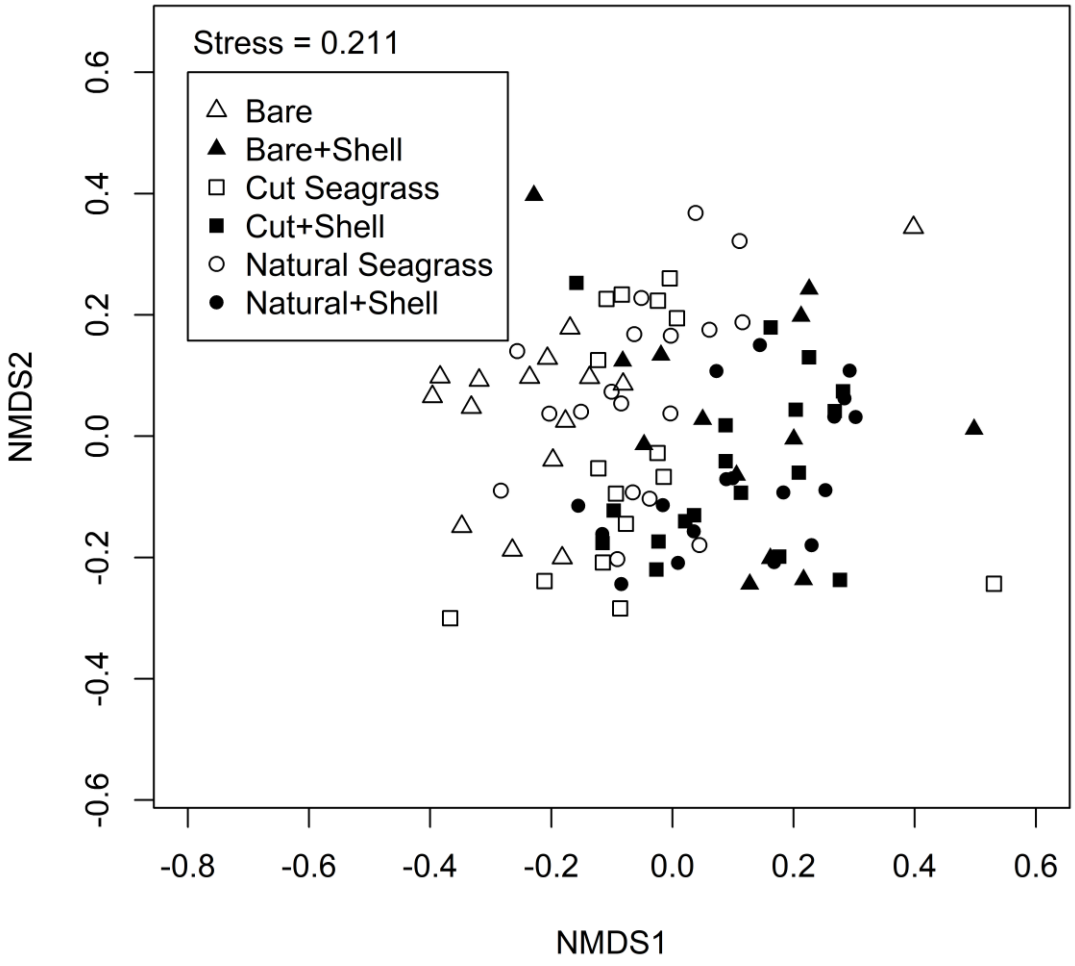
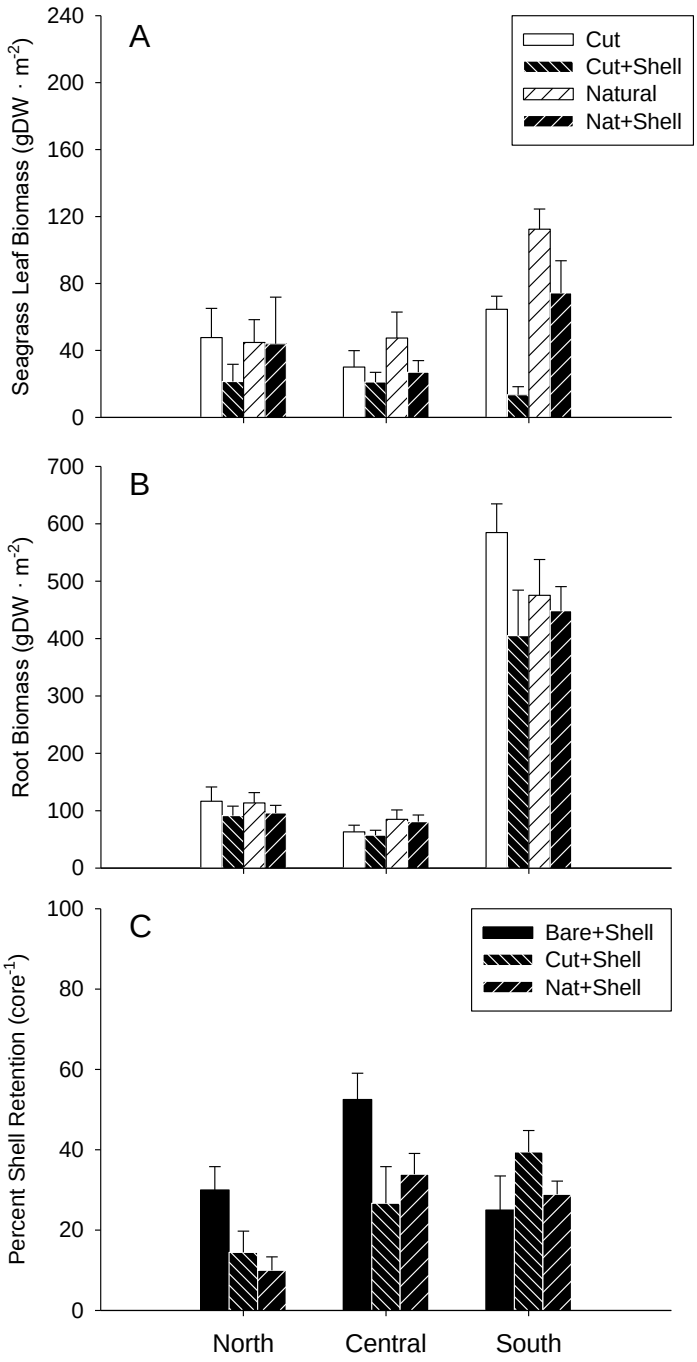


Figure 5.9 Seagrass (A) leaf biomass, (B) root and rhizome biomass, and (C) shell retention, from an experiment conducted in six estuaries from three regions (North, Central, South) on the South Island of New Zealand. +Shell = presence of shells (adding 10-15 shells per plot). Habitat = bare sediments, seagrass habitat with leaves cut (Cut), and undisturbed natural (Nat) seagrass, black = presence of dead shells. Note that seagrass responses were only relevant to test in the seagrass habitat (and therefore excluded the bare mud habitat), whereas the shell retention response only was relevant to test in the shell addition treatment (and therefore excluded the Shell-test factor).



References

Abbe, G. 1988. Population structure of the American oyster, *Crassostrea virginica,* on an oyster bar in central Chesapeake Bay: changes associated with shell planting and increased recruitment. Journal of Shellfish Research **7**:33-40.

Altieri, A. H., Silliman, B. R., and Bertness, M. D. 2007. Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. The American Naturalist **169**:195-206.

Altieri, A. H., and Witman, J. D. 2014. Modular mobile foundation species as reservoirs of biodiversity. Ecosphere **5**:1-11.

Angelini, C., and Silliman, B. R. 2014. Secondary foundation species as drivers of trophic and functional diversity: evidence from a tree–epiphyte system. Ecology **95**:185-196.

Angelini, C., van der Heide, T., Griffin, J. N., Morton, J. P., Derksen-Hooijberg, M., Lamers, L. P., Smolders, A. J., and Silliman, B. R. 2015. Foundation species' overlap enhances biodiversity and multifunctionality from the patch to landscape scale in southeastern United States salt marshes. Proceedings of the Royal Society B **282**:20150421.

Aquino-Thomas, J., and Proffitt, C. E. 2014. Oysters *Crassostrea virginica* on red mangrove *Rhizophora mangle* prop roots: facilitation of one foundation species by another. Marine Ecology Progress Series **503**:177-194.

Bak, R. P. M. 1976. The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. Netherlands Journal of Sea Research **10**:285-337.

Beal, B. 1994. Effects of seagrass (*Zostera marina*) cover on growth and survival of softshell clams (*Mya arenaria*). Journal of Shellfish Research **13**:311-312.

Bertness, M. D. 1984. Ribbed mussels and *Spartina alterniflora* production in a New England salt marsh. Ecology **65**:1794-1807.

Beukema, J. 1982. Calcimass and carbonate production by molluscs on the tidal flats in the Dutch Wadden Sea: II the edible cockle, *Cerastoderma edule*. Netherlands Journal of Sea Research **15**:391-405.

Bially, A., and Macisaac, H. J. 2000. Fouling mussels (*Dreissena* spp.) colonize soft sediments in Lake Erie and facilitate benthic invertebrates. Freshwater Biology **43**:85-97.

Bishop, M. J., Fraser, J., and Gribben, P. E. 2013. Morphological traits and density of foundation species modulate a facilitation cascade in Australian mangroves. Ecology **94**:1927-1936.

Bishop, M. J., Morgan, T., Coleman, M. A., Kelaher, B. P., Hardstaff, L. K., and Evenden, R. W. 2009. Facilitation of molluscan assemblages in mangroves by the fucalean alga *Hormosira banksii*. Marine Ecology Progress Series **392**:111-122.

Bódis, E., Tóth, B., Szekeres, J., Borza, P., and Sousa, R. 2014. Empty native and invasive bivalve shells as benthic habitat modifiers in a large river. Limnologica-Ecology and Management of Inland Waters **49**:1-9.

Bologna, P. A., and Heck, K. L. 1999. Differential predation and growth rates of bay scallops within a seagrass habitat. Journal of Experimental Marine Biology and Ecology **239**:299-314.

Bologna, P. A., and Heck, K. L. 2000. Impacts of seagrass habitat architecture on bivalve settlement. Estuaries **23**:449-457.

Bologna, P. A. X., Fetzer, M. L., McDonnell, S., and Moody, E. M. 2005. Assessing the potential benthic–pelagic coupling in episodic blue mussel (*Mytilus edulis*) settlement events within eelgrass (*Zostera marina*) communities. Journal of Experimental Marine Biology and Ecology **316**:117-131.

Bonar, D. B., Coon, S. L., Walch, M., Weiner, R. M., and Fitt, W. 1990. Control of oyster settlement and metamorphosis by endogenous and exogenous chemical cues. Bulletin of Marine Science **46**:484-498.

Booth, D. M., and Heck Jr., K. L. 2009. Effects of the american oyster *Crassostrea virginica* on growth rates of the seagrass *Halodule wrightii*. Marine Ecology Progress Series **389**:117-126.

Borowitzka, M. A., Lavery, P. S., and van Keulen, M. 2006. Epiphytes of seagrasses. Pages 441-461 *in* A. W. D. Larkum, R. J. Orth, and C. M. Duarte, editors. Seagrasses: Biology, Ecology, and Conservation. Springer Netherlands, Dordrecht.

Boström, C., and Bonsdorff, E. 2000. Zoobenthic community establishment and habitat complexity the importance of seagrass shoot-density, morphology and physical disturbance for faunal recruitment. Marine Ecology Progress Series **205**:123-138.

Boström, C., Jackson, E. L., and Simenstad, C. A. 2006. Seagrass landscapes and their effects on associated fauna: a review. Estuarine, Coastal and Shelf Science **68**:383-403.

Brett, C. E., Parsons-Hubbard, K. M., Walker, S. E., Ferguson, C., Powell, E. N., Staff, G., Ashton-Alcox, K. A., and Raymond, A. 2011. Gradients and patterns of sclerobionts on experimentally deployed bivalve shells: synopsis of bathymetric and temporal trends on a decadal time scale. Palaeogeography, Palaeoclimatology, Palaeoecology **312**:278-304.

Brun, F. G., Vergara, J. J., Navarro, G., Hernández, I., and Pérez-Lloréns, J. L. 2003. Effect of shading by *Ulva rigida* canopies on growth and carbon balance of the seagrass *Zostera noltii*. Marine Ecology Progress Series **265**:85-96.

Bunnell, F. L., Houde, I., Johnston, B., and Wind, E. 2002. How dead trees sustain live organisms in western forests. PSW-GTR-181.

Butman, C. A. 1986. Larval settlement of soft-sediment invertebrates: Some predictions based on an analysis of near-bottom velocity profiles. Pages 487-513 *in* J. C. J. Nihoul, editor. Elsevier Oceanography Series. Elsevier.

Callaway, R., Desroy, N., Dubois, S. F., Fournier, J., Frost, M., Godet, L., Hendrick, V. J., and Rabaut, M. 2010. Ephemeral bio-engineers or reef-building polychaetes: How stable are aggregations of the tube worm *Lanice conchilega* (Pallas, 1766)? Integrative and Comparative Biology **50**:237-250.

Carroll, J., Gobler, C. J., and Peterson, B. J. 2008. Resource-restricted growth of eelgrass in New York estuaries: light limitation, and alleviation of nutrient stress by hard clams. Marine Ecology Progress Series **369**:51-62.

Carroll, J. M., and Peterson, B. J. 2013. Comparisons in demographic rates of bay scallops in eelgrass and the introduced alga, *Codium fragile*, in New York. Marine Biology **160**:1451-1463.

Chalmer, P. N., Hodgkin, E. P., and Kendrick, G. 1976. Benthic faunal changes in a seasonal estuary of south-western Australia. Records of the Western Australian Museum **4**:383-409.

Clements, J. C., and Chopin, T. 2016. Ocean acidification and marine aquaculture in North America: potential impacts and mitigation strategies. Reviews in Aquaculture **9**:326-341

Coen, L. D., Brumbaugh, R. D., Bushek, D., Grizzle, R., Luckenbach, M. W., Posey, M. H., Powers, S. P., and Tolley, S. 2007. Ecosystem services related to oyster restoration. Marine Ecology Progress Series **341**:303-307.

Coen, L. D., Dumbauld, B. R., and Judge, M. L. 2011. Expanding shellfish aquaculture: a review of the ecological services provided by and impacts of native and cultured bivalves in shellfish-dominated ecosystems. Pages 239-295 *in* S. E. Shumway, editor. Shellfish Aquaculture and the Environment. Wiley-Blackwell, Oxford, UK.

Coen, L. D., and Heck Jr., K. L. 1991. The interacting effects of siphon nipping and habitat on bivalve (*Mercenaria mercenaria* (L.)) growth in a subtropical seagrass (*Halodule wrightii* Aschers) meadow. Journal of Experimental Marine Biology and Ecology **145**:1-13.

Colombini, I., and Chellazi, L. 2003. Influence of marine allochthonous input on sandy beach communities. Oceanography and Marine Biology: An Annual Review **41**:115-159.

Commito, J. A., Commito, A. E., Platt, R. V., Grupe, B. M., Piniak, W. E. D., Gownaris, N. J., Reeves, K. A., and Vissichelli, A. M. 2014. Recruitment facilitation and spatial pattern formation in soft-bottom mussel beds. Ecosphere **5**:1-26.

Cummings, V. J., Thrush, S. F., Hewitt, J. E., and Turner, S. J. 1998. The influence of the pinnid bivalve *Atrina zelandica* (Gray) on benthic macroinvertebrate communities in soft-sediment habitats. Journal of Experimental Marine Biology and Ecology **228**:227-240.

Dame, R. F. 1979. The abundance, diversity and biomass of macrobenthos on North Inlet, South Carolina, intertidal oyster reefs. Pages 6-10 *in* Proceedings of the National Shellfisheries Association.

Dauer, D., Tourtellotte, G., and Ewing, R. 1982. Oyster shells and artificial worm tubes: the role of refuges in structuring benthic communities of the lower chesapeake bay. Internationale Revue der Gesamten Hydrobiologie und Hydrographie **67**:661-677.

Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. Pages 81-96 *in* Proceedings of the Colloquium on Conservation Problems in Antarctica. Allen Press Lawrence, Kansas, USA.

de Chantal, M., and Granström, A. 2007. Aggregations of dead wood after wildfire act as browsing refugia for seedlings of *Populus tremula* and *Salix caprea*. Forest Ecology and Management **250**:3-8.

Devinny, J. S., and Volse, L. A. 1978. Effects of sediments on the development of *Macrocystis pyrifera* gametophytes. Marine Biology **48**:343-348.

Dugan, J. E., Hubbard, D. M., McCrary, M. D., and Pierson, M. O. 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. Estuarine, Coastal and Shelf Science **58**:25-40.

Eggleston, D. B., Elis, W. E., Etherington, L. L., Dahlgren, C. P., and Posey, M. H. 1999. Organism responses to habitat fragmentation and diversity: habitat colonization by estuarine macrofauna. Journal of Experimental Marine Biology and Ecology **236**:107-132.

Ellison, A. M., Bank, M. S., Clinton, B. D., Colburn, E. A., Elliott, K., Ford, C. R., Foster, D. R., Kloeppel, B. D., Knoepp, J. D., and Lovett, G. M. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment **3**:479-486.

Erlandson, J. M. 2001. The archaeology of aquatic adaptations: paradigms for a new millennium. Journal of Archaeological Research **9**:287-350.

Fonseca, M. S., and Cahalan, J. A. 1992. A preliminary evaluation of wave attenuation by four species of seagrass. Estuarine, Coastal and Shelf Science **35**:565-576.

Fonseca, M. S., Fisher, J. S., Zieman, J. C., and Thayer, G. W. 1982. Influence of the seagrass, *Zostera marina* L., on current flow. Estuarine, Coastal and Shelf Science **15**:351-364.

Franklin, J. F., Shugart, H. H., and Harmon, M. E. 1987. Tree death as an ecological process. BioScience **37**:550-556.

Gagné, F., Blaise, C., Pellerin, J., Fournier, M., Durand, M. J., and Talbot, A. 2008. Relationships between intertidal clam population and health status of the soft-shell clam *Mya arenaria* in the St. Lawrence Estuary and Saguenay Fjord (Québec, Canada). Environment International **34**:30-43.

Gain, I. E., Brewton, R. A., Reese Robillard, M. M., Johnson, K. D., Smee, D. L., and Stunz, G. W. 2016. Macrofauna using intertidal oyster reef varies in relation to position within the estuarine habitat mosaic. Marine Biology **164**:8.

Gardner, J. 2004. A historical perspective of the genus *Mytilus* (Bivalvia: Mollusca) in New Zealand: multivariate morphometric analyses of fossil, midden and contemporary blue mussels. Biological Journal of the Linnean Society **82**:329-344.

Gaylord, B., Hill, T. M., Sanford, E., Lenz, E. A., Jacobs, L. A., Sato, K. N., Russell, A. D., and Hettinger, A. 2011. Functional impacts of ocean acidification in an ecologically critical foundation species. The Journal of Experimental Biology **214**:2586-2594.

Gilad, E., von Hardenberg, J., Provenzale, A., Shachak, M., and Meron, E. 2004. Ecosystem engineers: from pattern formation to habitat creation. Physical Review Letters **93**:098105.

Grabowski, J. H., and Peterson, C. H. 2007. Restoring oyster reefs to recover ecosystem services. Pages 281-298 *in* C. K, B. JE, W. W, and H. A, editors. Ecosystem Engineers: Plants to Protists. Academic Press, New York, NY.

Grange, K. R. 1979. Soft-bottom macrobenthic communities of Manukau Harbour, New Zealand. New Zealand Journal of Marine and Freshwater Research **13**:315-329.

Green, M. A., Waldbusser, G. G., Reilly, S. L., Emerson, K., and O'Donnell, S. 2009. Death by dissolution: sediment saturation state as a mortality factor for juvenile bivalves. Limnology and Oceanography **54**:1037-1047.

Gregory, S. V., Swanson, F. J., McKee, W. A., and Cummins, K. W. 1991. An ecosystem perspective of riparian zones. BioScience **41**:540-551.

Greinert, J., Lewis, K. B., Bialas, J., Pecher, I. A., Rowden, A., Bowden, D. A., De Batist, M., and Linke, P. 2010. Methane seepage along the Hikurangi Margin, New Zealand: overview of studies in 2006 and 2007 and new evidence from visual, bathymetric and hydroacoustic investigations. Marine Geology **272**:6-25.

Gribben, P. E., Byers, J. E., Clements, M., McKenzie, L. A., Steinberg, P. D., and Wright, J. T. 2009. Behavioural interactions between ecosystem engineers control community species richness. Ecology Letters **12**:1127-1136.

Gribben, P. E., Kimbro, D. L., Vergés, A., Gouhier, T. C., Burrell, S., Garthwin, R. G., Cagigas, M. L., Tordoff, Y., and Poore, A. G. B. 2017. Positive and negative interactions control a facilitation cascade. Ecosphere **8**:e02065.

Gribben, P. E., and Wright, J. T. 2006. Invasive seaweed enhances recruitment of a native bivalve: roles of refuge from predation and the habitat choice of recruits. Marine Ecology Progress Series **318**:177-185.

Grizzle, R. E., Short, F. T., Newell, C. R., Hoven, H., and Kindblom, L. 1996. Hydrodynamically induced synchronous waving of seagrasses:'monami'and its possible effects on larval mussel settlement. Journal of Experimental Marine Biology and Ecology **206**:165-177.

Gutiérrez, J. L., Jones, C. G., Strayer, D. L., and Iribarne, O. O. 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos **101**:79-90.

Hacker, S. D., and Gaines, S. D. 1997. Some implications for direct positive interactions for community species diversity. Ecology **78**:1990-2003.

Harmon, M. E., Franklin, J. F., Swanson, F. J., Sollins, P., Gregory, S. V., Lattin, J. D., Anderson, N. H., Cline, S. P., Aumen, N. G., Sedell, J. R., Lienkaemper, G. W., Cromack, K., and Cummins, K. W. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research **15**:133-302.

Hastings, A., Byers, J. E., Crooks, J. A., Cuddington, K., Jones, C. G., Lambrinos, J. G., Talley, T. S., and Wilson, W. G. 2007. Ecosystem engineering in space and time. Ecology Letters **10**:153-164.

Healey, D., and Hovel, K. A. 2004. Seagrass bed patchiness: effects on epifaunal communities in San Diego Bay, USA. Journal of Experimental Marine Biology and Ecology **313**:155-174.

Helama, S., and Hood, B. C. 2011. Stone age midden deposition assessed by bivalve sclerochronology and radiocarbon wiggle-matching of *Arctica islandica* shell increments. Journal of Archaeological Science **38**:452-460.

Hendriks, I. E., Cabanellas-Reboredo, M., Bouma, T. J., Deudero, S., and Duarte, C. M. 2011. Seagrass meadows modify drag forces on the shell of the fan mussel *Pinna nobilis*. Estuaries and Coasts **34**:60-67.

Hewitt, J. E., Thrush, S. F., Halliday, J., and Duffy, C. 2005. The importance of small-scale habitat structure for maintaining beta diversity. Ecology **86**:1619-1626.

Hollever, J., and Bolton-Ritchie, L. 2016. Broad scale mapping of the estuary of the Heathcote and Avon rivers/Ihutai. Environment Canterbury.

Holmer, M., Frederiksen, M. S., and Møllegaard, H. 2005. Sulfur accumulation in eelgrass (*Zostera marina*) and effect of sulfur on eelgrass growth. Aquatic Botany **81**:367-379.

Horvath, T. G., Martin, K. M., and Lamberti, G. A. 1999. Effect of zebra mussels, *Dreissena polymorpha*, on macroinvertebrates in a lake-outlet stream. The American Midland Naturalist **142**:340-347.

Ilarri, M. I., Souza, A. T., Antunes, C., Guilhermino, L., and Sousa, R. 2014. Influence of the invasive asian clam *Corbicula fluminea* (Bivalvia: Corbiculidae) on estuarine epibenthic assemblages. Estuarine, Coastal and Shelf Science **143**:12-19.

Irlandi, E. 1996. The effects of seagrass patch size and energy regime on growth of a suspension-feeding bivalve. Journal of Marine Research **54**:161-185.

Irlandi, E. A. 1997. Seagrass patch size and survivorship of an infaunal bivalve. Oikos **78**:511-518.

Irlandi, E. A., Orlando, B. A., and Ambrose Jr, W. G. 1999. Influence of seagrass habitat patch size on growth and survival of juvenile bay scallops, *Argopecten irradians concentricus* (Say). Journal of Experimental Marine Biology and Ecology **235**:21-43.

Irlandi, E. A., and Peterson, C. H. 1991. Modification of animal habitat by large plants: mechanisms by which seagrasses influence clam growth. Oecologia **87**:307-318.

Jaap, W. C. 2000. Coral reef restoration. Ecological Engineering **15**:345-364.

Jones, C. G., Lawton, J. H., and Shachak, M. 1994. Organisms as ecosystem engineers. Oikos **69**:373-386.

Jones, C. G., Lawton, J. H., and Shachak, M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology **78**:1946-1957.

Kainamu-Murchie, A. A., Marsden, I. D., Tau, R. T. M., Gaw, S., and Pirker, J. 2018. Indigenous and local peoples' values of estuarine shellfisheries: moving towards holistic-based catchment management. New Zealand Journal of Marine and Freshwater Research **52**:526-541.

Kidwell, S. M. 1986. Taphonomic feedback in miocene assemblages: testing the role of dead hardparts in benthic communities. Palaios **1**:239-255.

Kidwell, S. M., and Jablonski, D. 1983. Taphonomic feedback ecological consequences of shell accumulation. Pages 195-248 *in* M. J. S. Tevesz and P. L. McCall, editors. Biotic Interactions in Recent and Fossil Benthic Communities. Springer US, Boston, MA.

Kirtley, D. W., and Tanner, W. F. 1968. Sabellariid worms: builders of a major reef type. Journal of Sedimentary Research **38**.

Lavery, P. S., Reid, T., Hyndes, G. A., and Van Elven, B. R. 2007. Effect of leaf movement on epiphytic algal biomass of seagrass leaves. Marine Ecology Progress Series **338**:97-106.

Lehnert, R. L., and Allen, D. M. 2002. Nekton use of subtidal oyster shell habitat in a southeastern U.S. Estuary. Estuaries **25**:1015-1024.

McClintock, J. B., Angus, R. A., McDonald, M. R., Amsler, C. D., Catledge, S. A., and Vohra, Y. K. 2009. Rapid dissolution of shells of weakly calcified Antarctic benthic macroorganisms indicates high vulnerability to ocean acidification. Antarctic Science **21**:449-456.

McConnaughey, T. A., and Gillikin, D. P. 2008. Carbon isotopes in mollusk shell carbonates. Geo-Marine Letters **28**:287-299.

Mills, V. S., and Berkenbusch, K. 2009. Seagrass (*Zostera muelleri*) patch size and spatial location influence infaunal macroinvertebrate assemblages. Estuarine, Coastal and Shelf Science **81**:123-129.

Munguia, P. 2007. Spatial structure of communities on dead pen shells (*Atrina rigida*) in sea grass beds. Marine Biology **152**:149-156.

Murray, J. W. 1983. Population dynamics of benthic foraminifera; results from the Exe Estuary, England. The Journal of Foraminiferal Research **13**:1-12.

Nagelkerken, I., Blaber, S. J. M., Bouillon, S., Green, P., Haywood, M., Kirton, L. G., Meynecke, J. O., Pawlik, J., Penrose, H. M., Sasekumar, A., and Somerfield, P. J. 2008. The habitat function of mangroves for terrestrial and marine fauna: a review. Aquatic Botany **89**:155-185.

Newell, R. I., and Koch, E. W. 2004. Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. Estuaries **27**:793-806.

NIWA. 2015. Investigating ocean acidification. Pages 13-21 Water & Atmosphere. NIWA, Wellington, New Zealand.

Olabarria, C., Incera, M., Garrido, J., and Rossi, F. 2010. The effect of wrack composition and diversity on macrofaunal assemblages in intertidal marine sediments. Journal of Experimental Marine Biology and Ecology **396**:18-26.

Orlova, M. I., and Panov, V. E. 2004. Establishment of the zebra mussel, *Dreissena polymorpha* (Pallas), in the Neva Estuary (Gulf of Finland, Baltic Sea): distribution, population structure and possible impact on local unionid bivalves. Pages 207-217 *in* H. Kautsky and P. Snoeijs, editors. Biology of the Baltic Sea: Proceedings of the 17th BMB Symposium, 25–29 november 2001, Stockholm, Sweden. Springer Netherlands, Dordrecht.

Orth, R. J., Heck, K. L., and van Montfrans, J. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries **7**:339-350.

Parker, L., Ross, P., O'Connor, W., Pörtner, H., Scanes, E., and Wright, J. 2013. Predicting the response of molluscs to the impact of ocean acidification. Biology **2**:651.

Peterson, B. J., and Heck Jr, K. L. 2001. Positive interactions between suspension-feeding bivalves and seagrass-a facultative mutualism. Marine Ecology Progress Series **213**:143-155.

Peterson, C. H., Summerson, H., and Duncan, P. 1984. The influence of seagrass cover on population structure and individual growth rate of a suspension-feeding bivalve, *Mercenaria mercenaria*. Journal of Marine Research **42**:123-138.

Pinkster, S., and Broodbakker, N. W. 1980. The influence of environmental factors on distribution and reproductive success of *Eulimnogammarus obtusatus* (Dahl, 1938) and other estuarine gammarids. Crustaceana. Supplement:225-241.

Posey, M. H., Alphin, T. D., Powell, C. M., and Townsend, E. 1999. Use of oyster reefs as habitat for epibenthic fish and decapods. Pages 229-237 *in* Luckenbach, M., Mann, R., Wesson, J. editors. Oyster reef habitat restoration: a synopsis and synthesis of approaches. Virginia Institute of Marine Science Press, Williamsburg, PA.Powell, E. N., Kraeuter, J. N., and Ashton-Alcox, K. A. 2006. How long does oyster shell last on an oyster reef? Estuarine, Coastal and Shelf Science **69**:531-542.

Powell, E. N., Staff, G. M., Davies, D. J., and Callender, W. R. 1989. Macrobenthic death assemblages in modern marine environments: formation, interpretation, and application. Reviews in Aquatic Sciences **1**:555-589.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reusch, T., Chapman, A., and Groger, J. 1994. Blue mussels *Mytilus edulis* do not interfere with eelgrass *Zostera marina* but fertilize shoot growth through biodeposition. Marine Ecology Progress Series **108**:265-282.

Reusch, T. B., and Williams, S. L. 1998. Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia*. Oecologia **113**:428-441.

Reusch, T. B. H., and Chapman, A. R. O. 1995. Storm effects on eelgrass (*Zostera marina* L.) and blue mussel (*Mytilus edulis* L.) beds. Journal of Experimental Marine Biology and Ecology **192**:257-271.

Ricciardi, A., Whoriskey, F. G., and Rasmussen, J. B. 1997. The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. Canadian Journal of Fisheries and Aquatic Sciences **54**:2596-2608.

Rodil, I. F., Olabarria, C., Lastra, M., and López, J. 2008. Differential effects of native and invasive algal wrack on macrofaunal assemblages inhabiting exposed sandy beaches. Journal of Experimental Marine Biology and Ecology **358**:1-13.

Schanz, A., Polte, P., and Asmus, H. 2002. Cascading effects of hydrodynamics on an epiphyte–grazer system in intertidal seagrass beds of the Wadden Sea. Marine Biology **141**:287-297.

Schejter, L., and Bremec, C. 2007. Benthic richness in the Argentine continental shelf: the role of *Zygochlamys patagonica* (Mollusca: Bivalvia: Pectinidae) as settlement substrate. Journal of the Marine Biological Association of the United Kingdom **87**:917-925.

Schiel, D. R., Wood, S. A., Dunmore, R. A., and Taylor, D. I. 2006. Sediment on rocky intertidal reefs: effects on early post-settlement stages of habitat-forming seaweeds. Journal of Experimental Marine Biology and Ecology **331**:158-172.

Schlawin, J. R., and Zahawi, R. A. 2008. 'Nucleating' succession in recovering neotropical wet forests: the legacy of remnant trees. Journal of Vegetation Science **19**:485-492.

Schöne, B. R., Wanamaker, A. D., Fiebig, J., Thébault, J., and Kreutz, K. 2011. Annually resolved δ13C shell chronologies of long-lived bivalve mollusks (*Arctica islandica*) reveal oceanic carbon dynamics in the temperate North Atlantic during recent centuries. Palaeogeography, Palaeoclimatology, Palaeoecology **302**:31-42.

Sedell, J. R., and Froggatt, J. L. 1984. Importance of streamside forests to large rivers: the isolation of the Willamette River, Oregon, USA, from its floodplain by snagging and streamside forest removal. Internationale Vereinigung fur Theoretische und Angewandte Limnologie **22**:1828-1834.

Shreffler, D. K., and Griffin, K. 2000. Ecological interactions among eelgrass, oysters, and burrowing shrimp in Tillamook Bay, Oregon Year 2 (1999) Report. Pages 1-53 *in* T. C. P. Partnership, editor. Tillamook County Performance Partnership, Garabaldi, OR.

Smith, I. 2013. Pre-european Maori exploitation of marine resources in two New Zealand case study areas: species range and temporal change Journal of the Royal Society of New Zealand **43**:1-37.

Sousa, R., Gutiérrez, J., and Aldridge, D. 2009. Non-indigenous invasive bivalves as ecosystem engineers. Biological Invasions **11**:2367-2385.

Strayer, D. L., Caraco, N. F., Cole, J. J., Findlay, S., and Pace, M. L. 1999. Transformation of freshwater ecosystems by bivalves. BioScience **49**:19-27.

Strayer, D. L., and Malcom, H. M. 2007. Shell decay rates of native and alien freshwater bivalves and implications for habitat engineering. Freshwater Biology **52**:1611-1617.

Summerhayes, S. A., Bishop, M. J., Leigh, A., and Kelaher, B. P. 2009. Effects of oyster death and shell disarticulation on associated communities of epibiota. Journal of Experimental Marine Biology and Ecology **379**:60-67.

Surge, D. M., Lohmann, K. C., and Goodfriend, G. A. 2003. Reconstructing estuarine conditions: oyster shells as recorders of environmental change, Southwest Florida. Estuarine, Coastal and Shelf Science **57**:737-756.

Tallis, H. M., Ruesink, J. L., Dumbauld, B., Hacker, S., and Wisehart, L. M. 2009. Oysters and aquaculture practices affect eelgrass density and productivity in a Pacific Northwest estuary. Journal of Shellfish Research **28**:251-261.

Tamburri, M. N., Zimmer-Faust, R. K., and Tamplin, M. L. 1992. Natural sources and properties of chemical inducers mediating settlement of oyster larvae: a re-examination. The Biological Bulletin **183**:327-338.

Thomsen, M. S. 2004. Species, thallus size and substrate determine macroalgal break force and break location in a low-energy soft-bottom lagoon. Aquatic Botany **80**:153-161.

Thomsen, M. S., Alestra, T., Brockerhoff, D., Lilley, S. A., South, P. M., and Schiel, D. R. 2018a. Modified kelp seasonality and invertebrate diversity where an invasive kelp co-occurs with native mussels. Marine Biology **165**:173.

Thomsen, M. S., Altieri, A. H., Angelini, C., Bishop, M. J., Gribben, P. E., Lear, G., He, Q., Schiel, D. R., Silliman, B. R., South, P. M., Watson, D. M., Wernberg, T., and Zotz, G. 2018b. Secondary foundation species enhance biodiversity. Nature Ecology & Evolution **2**:634-639.

Thomsen, M. S., Hildebrand, T., South, P. M., Foster, T., Siciliano, A., Oldach, E., and Schiel, D. R. 2016. A sixth-level habitat cascade increases biodiversity in an intertidal estuary. Ecology and Evolution **6**:8291-8303.

Thomsen, M. S., Wernberg, T., Altieri, A., Tuya, F., Gulbransen, D., McGlathery, K. J., Holmer, M., and Silliman, B. R. 2010. Habitat cascades: the conceptual context and global relevance of

facilitation cascades via habitat formation and modification. Integrative and Comparative Biology **50**:158-175.

Thrush, S. F., Hewitt, J. E., Funnell, G. A., Cummings, V. J., Ellis, J., Schultz, D., Talley, D., and Norkko, A. 2001. Fishing disturbance and marine biodiversity: the role of habitat structure in simple soft-sediment systems. Marine Ecology Progress Series **223**:277-286.

Tolley, S. G., and Volety, A. K. 2005. The role of oysters in habitat use of oyster reefs by resident fishes and decapod crustaceans. Journal of Shellfish Research **24**:1007-1012.

Tsai, C., Yang, S., Trimble, A. C., and Ruesink, J. L. 2010. Interactions between two introduced species: *Zostera japonica* (dwarf eelgrass) facilitates itself and reduces condition of *Ruditapes philippinarum* (Manila clam) on intertidal flats. Marine Biology **157**:1929-1936.

Turner, E. J., Zimmer-Faust, R. K., Palmer, M. A., Luckenbach, M., and Pentchef, N. D. 1994. Settlement of oyster (*Crassostrea virginica*) larvae: effects of water flow and a water-soluble chemical cue. Limnology and Oceanography **39**:1579-1593.

Umar, M. J., McCook, L. J., and Price, I. R. 1998. Effects of sediment deposition on the seaweed *Sargassum* on a fringing coral reef. Coral Reefs **17**:169-177.

van der Heide, T., Govers, L. L., de Fouw, J., Olff, H., van der Geest, M., van Katwijk, M. M., Piersma, T., van de Koppel, J., Silliman, B. R., Smolders, A. J., and van Gills, J. A. 2012. A three-stage symbiosis forms the foundation of seagrass ecosystems. Science **336**:1432-1434.

Vinther, H. F., and Holmer, M. 2008. Experimental test of biodeposition and ammonium excretion from blue mussels (*Mytilus edulis*) on eelgrass (*Zostera marina*) performance. Journal of Experimental Marine Biology and Ecology **364**:72-79.

Vinther, H. F., Laursen, J. S., and Holmer, M. 2008. Negative effects of blue mussel (*Mytilus edulis*) presence in eelgrass (*Zostera marina*) beds in Flensborg Fjord, Denmark. Estuarine, Coastal and Shelf Science **77**:91-103.

Wagner, E., Dumbauld, B. R., Hacker, S. D., Trimble, A. C., Wisehart, L. M., and Ruesink, J. L. 2012. Density-dependent effects of an introduced oyster, *Crassostrea gigas*, on a native intertidal seagrass, *Zostera marina*. Marine Ecology Progress Series **468**:149-160.

Waldbusser, G. G., Powell, E. N., and Mann, R. 2013. Ecosystem effects of shell aggregations and cycling in coastal waters: an example of Chesapeake Bay oyster reefs. Ecology **94**:895-903.

Waldbusser, G. G., Steenson, R. A., and Green, M. A. 2011. Oyster shell dissolution rates in estuarine waters: effects of pH and shell legacy. Journal of Shellfish Research **30**:659-669.

Wall, C. C., Peterson, B. J., and Gobler, C. J. 2008. Facilitation of seagrass *Zostera marina* productivity by suspension-feeding bivalves. Marine Ecology Progress Series **357**:165-174.

Wasson, K. 2010. Informing Olympia oyster restoration: evaluation of factors that limit populations in a California estuary. Wetlands **30**:449-459.

Welladsen, H. M., Southgate, P. C., and Heimann, K. 2010. The effects of exposure to near-future levels of ocean acidification on shell characteristics of *Pinctada fucata* (Bivalvia: Pteriidae). Molluscan Research **30**:125.

Wilbur, K. M. 1972. Shell formation in mollusks. Chemical Zoology **7**:103-145.

Williams, l., Cryer, M., McKenzie, l., Smith, M. D., Watson, T. G., MacKay, G., and Tasker, R. 2006. Biomass survey and stock assessment of cockles (*Austrovenus stutchburyi*) on Snake Bank, Whangarei Harbour, 2005. *in* NIWA Research.

Yao, Z., Xia, M., Li, H., Chen, T., Ye, Y., and Zheng, H. 2014. Bivalve shell: not an abundant useless waste but a functional and versatile biomaterial. Critical Reviews in Environmental Science and Technology **44**:2502-2530.

Supplementary Material

Figure S1A. An example of the Cut seagrass treatment (ca. 15 cm diameter). Note the centre peg to delineate the treatment plot, and the seagrass leaves cut to the sediment surface.

Figure S1B. An example of the Cut+Shell seagrass treatment (ca. 15 cm diameter). Note that shells were haphazardly inserted partially into the sediment around the centre peg, and that the seagrass removal treatment expands past the shell diameter.

Figure S1C. An example of the natural seagrass treatment (ca. 15 cm diameter). This was considered the control treatment; seagrass leaves were left at full length and natural densities. Note the centre peg to delineate the experimental plot.

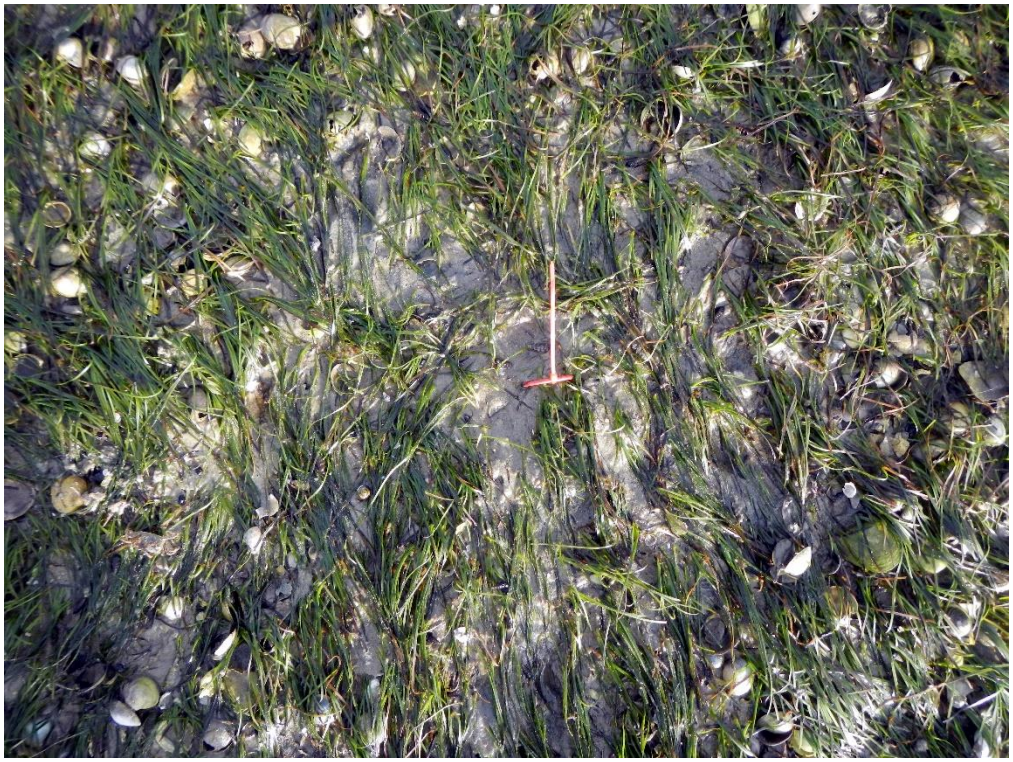


Figure S1D. An example of the Natural+Shell seagrass treatment (ca. 15 cm diameter). Shells were haphazardly inserted partially into the sediment around the centre peg.

CHAPTER 6 ESTUARINE SNAILS AS MOBILE FOUNDATION SPECIES: DISTRIBUTIONS, GRAZING RATES, AND HABITAT FORMATION

Abstract

Foundation species are ecologically important organisms that modify community structure, create habitat, and provide ecosystem services. Most foundation species are sessile, like seagrass or trees, but some mobile organisms may also play this important ecological role. For example, in soft-bottom estuarine systems, mobile snails can create habitat for other sessile species (bottom-up effects) and modify communities by grazing on seaweed, seagrass, and biofilms (top-down effects). However, few studies have documented this dual ecological function. The objective of this study was to document distribution patterns and top-down and bottom-up effects of two common, co-occurring, estuarine trochid snails in New Zealand, *Micrelenchus huttonii* and *Diloma nigerrimum*. These snails, although similar, could potentially have different effects on the environment around them. First, distribution patterns were quantified from cores collected across different latitudes, estuaries, tidal elevation levels, seasons, and habitats. Then, top-down effects were evaluated through choice and no-choice lab and field experiments. Finally, bottom-up effects were quantified by counting epibiota on >13,000 snails of varying sizes. *Diloma* and *Micrelenchus* were found in 12 and 11 of the 15 sampled estuaries respectively, with highest mean density of 441 ± 95 and 4146 ± 1205 snails m^{-2}, respectively. Seasonal surveys from the Avon-Heathcote estuary showed year-round presence of both *Diloma* and *Micrelenchus*, with higher densities of *Diloma* in summer and *Micrelenchus* in winter. *Micrelenchus* had stronger top-down effects than *Diloma* in all experiments, with stronger grazing on the coarsely branched seaweed *Gracilaria* than on the sheet-forming seaweed *Ulva* (up to 22 times more in the lab and 12 times more in the field). *Micrelenchus* also provided habitat to 3 times more epibionts than *Diloma* and had more epiphytized shells (57% vs 43%), although *Diloma* had more *Ulva* recruits per shell (3.2 ± 0.6 vs 0.9 ± 0.1). These differences between two co-occurring, similar looking trochid snails could be caused by different anatomical features (radula adapted to grazing micro- vs. macroalga) and thus different foraging preferences, as well as different physiological stress-tolerance to desiccation and sedimentation. This study shows that both *Diloma* and *Micrelenchus* are abundant and common in sampled estuaries on the South Island of New Zealand, provide positive effects to epibiotic communities through habitat creation, and negative effects through grazing simultaneously.

Introduction

Foundation species are ecologically important organisms that modify biological communities via habitat creation, stress reduction, and provision of ecosystem services (Dayton 1972, Ellison et al. 2005). The most common foundation species are sessile primary producers such as trees, kelps, mangroves, seagrass, and cacti (Ellison et al. 2005, Villegas et al. 2008, Angelini et al. 2011). These organisms change the landscape through bottom-up processes ranging from the formation of small patches of nursery desert cacti to covering large geographic areas such as temperate forests (Angelini et al. 2011). However, small mobile organisms such as decorator crabs (Dick et al. 1998, Fernández et al. 1998), sea urchins (Gutt and Schickan 1998, Linse et al. 2008, Altieri and Witman 2014), and snails (Wernberg et al. 2010, Thomsen et al. 2016) can also be foundation species and provide habitat to communities of associated organisms. Communities associated with mobile foundation species can be rich and diverse and can actas mobile pockets of biodiversity moving through the ecosystems they inhabit (Wernberg et al. 2010, Thyrring et al. 2013, Altieri and Witman 2014). Snails are particularly important marine mobile foundation species because their shells can provide hard substrate (Voight and Walker 1995, Yakovis et al. 2008) for sessile flora (seaweeds) and fauna (such as barnacles, limpets, or bryozoans) to settle on (i.e., 'epibiosis') (Schmitt et al. 1983, Buschbaum and Reise 1999, Thomsen et al. 2016). Some snails support entire communities of sessile seaweed and animals. For example, in Australia *Turbo torquatus* hosted 13 different taxa of macroalgae on their shells (Wernberg et al. 2010), *Battilaria australis* hosted ca. 1 billion epiphytic *Gracilaria comosa* fronds (Thomsen et al. 2010b), and the deep-sea trochid snail *Gaza* spp. was inhabited by nine different types of epibionts including bryozoans, foraminiferans, barnacles, worms, and egg capsules of snails (Voight and Walker 1995).

Mobile foundation species such as snails not only facilitate epibiont communities through bottom-up habitat provision, but they can also modify community structures and processes through negative top-down effects such as predation or herbivory. For example, herbivorous snails can consume juvenile and adult macroalgae, thereby controlling community structures of kelp and fucoid beds (Bertness et al. 1983, Johnson and Mann 1986, Brönmark 1989, Altieri et al. 2009, Krumhansl and Scheibling 2011). Although grazing rates of snails often are lower than those of amphipods and isopods (Geertz-Hansen et al. 1993, Hauxwell et al. 1998), snails still exert considerable consumer pressures in coastal areas such as estuaries and

marshes (Haines and Montague 1979, Giannotti and McGlathery 2001, Fredriksen et al. 2004, Silliman et al. 2005, Thomsen et al. 2009a, Guidone et al. 2010, McLenaghan et al. 2011, Guidone et al. 2012, Thomsen et al. 2013, Guidone et al. 2014, Guidone et al. 2015).

Despite the apparent dual importance of mobile foundation species as controllers of biodiversity and ecosystem function through bottom-up and top-down processes, I am not aware of studies that have quantified both processes in combination. I addressed this research gap by quantifying (a) spatio-temporal distribution patterns (b) top-down trophic effects, and (c) epibiotic community composition, of two morphological similar trochids commonly found in estuaries of the South Island of New Zealand, *Micrelenchus huttonii* and *Diloma nigerrimum* (hereafter *Diloma* and *Micrelenchus*, Figure 1). I hypothesized that:

1. *Micrelenchus* and *Diloma* are more abundant in the north of the South Island than in in the south, due to warmer climate, and *Micrelenchus* is more abundant than *Diloma* across these regions because of its smaller size (Logan 1976, Jones et al. 2005, Andersen and Beyer 2006).
2. *Micrelenchus* is more abundant in the subtidal zone within seaweed habitats (Choat and Schiel 1982, Taylor 1997), while *Diloma* is more abundant in the intertidal zone and on bare sediments (Logan 1976, Jones et al. 2005).
3. Both species are more abundant in summer than in winter because of higher availability of micro- and macroalgal food (Lavery et al. 1991, Hauxwell et al. 1998).
4. *Micrelenchus* exerts higher grazing pressures than *Diloma* on seaweed because it is commonly associated with this type of biogenic habitat (see hypothesis 2).
5. *Diloma* has higher per-capita abundance and richness of epibiota than *Micrelenchus* because its larger shell provides more settling substrate to epibionts; Smyth and Roberts (2010), Thyrring et al. (2015).

Methods

Distribution

Spatial survey

To quantify large scale distribution patterns of the two snail species, 15 estuaries were sampled in 2016 on the South Island of New Zealand (Figure 6.1). , Six northern estuaries were sampled in the Tasman-Golden Bay area (northern region) in April 2016: Ruataniwha Inlet (40°39'10.2"S 172°40'35.5"E), Puponga Coast (40°31'36.1"S 172°44'03.6"E), Nelson

Haven (41°13'51.4"S 173°18'33.4"E), Delaware Bay (41°10'05.6"S 173°26'33.6"E), Okiwa Bay (41°15'54.8"S 173°54'57.2"E) and Ngakuta Bay (41°16'22.6"S 173°57'48.4"E). Six southern estuaries were sampled in October 2016 in the Otago-Southland area (southern region): Portobello Bay (45°49'21.6"S 170°39'58.3"E), Papanui Inlet (45°50'32.7"S 170°41'33.0"E), Dowling Bay (45°47'18.9"S 170°39'46.8"E), Catlins River Estuary (46°28'47.3"S 169°41'17.3"E), Jacob's River Estuary (46°20'52.7"S 168°00'56.3"E), and New River Estuary (46°25'47.6"S 168°20'18.3"E). Finally, three estuaries were sampled halfway through this latitudinal gradient, in the Canterbury region (central region): the Avon-Heathcote Estuary (43°32'58.1"S 172°44'33.6"E), Duvauchelle Bay (43°45'11.4"S 172°55'44.6"E), and Robinsons Bay (43°45'51.9"S 172°57'28.6"E).

In each estuary, three replicate circular cores (9 cm diameter × 10 cm depth) were collected from four different habitats; bare (unvegetated) sediment, sediments covered with the seaweed *Ulva* spp. (and/or *Gracilaria chilensis*), sediments covered with the seagrass *Zostera muelleri*, or sediments covered with both *Zostera* and *Ulva* (and/or *Gracilaria*). If an estuary contained more than one seaweed species, cores were collected for each of them. Sampled cores were placed into labelled 1 mm mesh bags, rinsed in the field to remove sediments, and placed in a -20 ˚C freezer within 4 hours of sampling. Cores were collected from both the mid intertidal and the shallow subtidal (this consists of low-tidal areas with puddles consistently having water) zones. The minimum number of cores per estuary was thereby 24 (4 habitat types × 2 elevation levels × 3 replicates). In the lab, thawed cores were washed through a 1 mm sieve to remove any remaining sediment, and the sieve was rinsed into a sorting tray. *Diloma nigerrimum* and *Micrelenchus huttonii* were counted and recorded, and abundances converted to densities per m^2. A Spearman's Rank correlation, corrected for tied data points, was used to test for relationships between densities of *Micrelenchus* and *Diloma*. Factorial analysis of variance (ANOVA) tested for differences in *Diloma* and *Micrelenchus* densities between sampled regions, estuaries, tidal elevations, and presence/absence of seagrass and seaweed. I did not test for differences between the two snails with ANOVA because the ranked correlation test was significant (see Results section) highlighting that the abundance of the two species was not statistically independent of each other. Variance homogeneity was checked with Levene's test (in the R-package *'car'*). If the assumption was violated, transformations were attempted (log 10 or square-root) and rechecked. If transformations could not remove variance heterogeneity, untransformed data were used, and alpha was reduced from 0.05 to 0.01. Tukey's Honestly Significant Difference post hoc tests were used

following significant results. Statistical analyses were performed in R version 3.5.0 (R Core Team 2017).

Seasonal survey

A two-year seasonal survey was conducted in the Avon-Heathcote Estuary, Christchurch, New Zealand from 2014-2016 to quantify seasonal patterns in the abundance of the two study species. Samples were collected two times each in summer and winter (4 times a year), at two sites with extensive seagrass beds, Plover and Tern Street. Tern Street is ca. 800 m closer to the oceanic inlet. Within each site, two replicates of the same four habitat types sampled as part of the spatial survey were collected from the same two elevation levels: bare sediment, *Ulva* on sediment, seagrass bed, and *Ulva* present in seagrass bed, corresponding to 16 cores per site per sample event. Cores were collected, processed and data analysed as described for the spatial survey; Spearman rank correlation tested for relationships between *Diloma* and *Micrelenchus* densities and factorial ANOVA tested for effects of season (after pooling within seasonal sampling events), sample site, tidal elevation, presence/absence of seagrass, presence/absence of seaweed, and snail taxa. Snail taxa were included as a test factor because the ranked correlation test was not significant, suggesting that the abundance of the two species was statistically independent of each other (see Results section).

Top-down grazing effects

Laboratory no-choice experiments

A laboratory no-choice grazing experiment was set up to to quantify the grazing patterns and rates of the two study species. The experiment was carried out in a temperature-controlled room (13°C) with a 12-hour light-dark cycle. Microcosms were created in 380 mL clear plastic bottles covered with translucent lids that allowed air exchange but no snail escape. Each microcosm was filled with filtered saline water at 30 ppt (corresponding to conditions in Avon-Heathcote Estuary where snails were collected). The experiment tested grazing rates between snail species (*Diloma*, *Micrelenchus*), among snail densities (0, 2, or 10 snails) and on food type (*Zostera muelleri*, *Gracilaria chilensis*, or *Ulva* spp.). Each snail treatment was offered one of three plant food-choices: the seagrass *Zostera muelleri*, the green, flat seaweed *Ulva* spp., or the red, branched seaweed *Gracilaria chilensis* (hereafter *Zostera*, *Ulva*, and *Gracilaria*) for a total of 15 treatment combinations (n = 6). Snails and plant material were collected at the same time and washed in filtered seawater to remove any detectable sediment

and inhabitants. Plant material was blotted with a paper towel and weighed before being added to microcosms. Approximately 0.50 g (wet weight) of plant material was added to each container. The experiment ran for 10 days, and water was changed every third day. At the end of the experiment, remaining plant material was collected, blotted, and weighed to determine final wet weight. Plant growth rates (μ) and snail grazing rates (g) were calculated following the equations described by Nejrup and Pedersen (2010):

$$\text{Eq 1. } \mu = \frac{(lnFW_t - lnFW_0)}{t}$$

$$\text{Eq 2. } g = \bar{\mu}_c - \mu_G$$

where μ is the relative growth rate of the seaweed or seagrass, FW_t is the initial wet-weight biomass, FW_0 is the final wet-weight biomass, t is the incubation time, g is the grazing rate, μ_c is the plant growth rate without snails, and μ_G is the plant growth rate in the presence of snails. Factorial ANOVA tested if grazing rates differed between snail taxa, food type, and snail abundance. Assumption tests and post-hoc analyses were conducted as described for the spatial survey.

Laboratory food-choice experiment

Grazing was only detectable at the high snail densities in the no-choice grazing experiment, and therefore only the 10-snail density was used in a follow up food-choice experiment. This experiment also included sediment as an alternative food-choice (but excluded *Zostera* because the previous experiment found no grazing effect on this species). Orthogonal test factors included snail species (controls with 0 snails, 10 *Micrelenchus*, 10 *Diloma*), plant food source (c. 0.5 g of wet *Ulva*, *Gracilaria*, *Ulva+Gracilaria*) and sediments (± adding 2 cm sediment) corresponding to 18 treatment combinations (n = 6). For the combined *Ulva+Gracilaria* treatment, 0.5 g of each species was added for a total of 1.0 g seaweed biomass. In the *Ulva+Gracilaria* treatment, the seaweed being analyzed is shown in parentheses after the treatment; that is, 'U+G (G)' is the grazing rates on *Gracilaria* in the *Ulva+Gracilaria* treatment. Sediment was added to the experiment to mimic estuarine conditions and because snails may graze on sedimentary benthic microalgae. Oxygenated, sandy surface sediment was collected from the same site where snails and plant material were collected in Avon-Heathcote Estuary. The sediment was returned to the lab, rinsed with seawater to mix it and remove invertebrates, and then half of the microcosms were filled to 2 cm with sediments. Other experimental conditions, procedures and analyses were as

described in the previous experiment. Factorial ANOVA tests were used to test if grazing rates differed between snail taxa, food type (with choices), and presence or absence of sediment. Assumption testing and post-hoc analyses were done as described for the spatial survey.

Field experiment of grazing rates of Micrelenchus

Finally, grazing of *Micrelenchus* was tested under natural field conditions (*Diloma* was excluded from the field experiment because of low grazing rates in the laboratory experiments). The plastic bottles used in the lab-experiments were attached to stakes and installed on the southern side of the Avon-Heathcote Estuary, in the low intertidal zone in an area with no seagrass or drift seaweed. Each bottle was covered with mesh to allow light, water, and sediment to enter, but keep seaweed and snails inside, and had holes on the side walls to allow water to drain out at low tide. For this experiment, two snail treatments (control and 10 *Micrelenchus*) were crossed with three seaweed treatments (c. 0.5 g of wet *Ulva, Gracilaria, Ulva+Gracilaria*) (n = 5). For the combined *Ulva+Gracilaria* treatment, ~0.5 g of each was added for a total of 1.0 g seaweed biomass. Treatments were randomly assigned to each bottle and bottles were separated by at least 0.5 m in the field. All other experimental conditions, procedures and analyses were as described in the previous experiments. ANOVA tested if grazing rates differed between food type (with choices). Assumption testing and post-hoc tests were completed as described for the spatial survey.

Bottom-up habitat provision

A total of 1,543 *Diloma* and 11,939 *Micrelenchus* were haphazardly collected along the eastern spit and along the southern side of the estuary (to include multiple habitats such as mud, seaweed, seagrass, and silt) of the Avon-Heathcote throughout 2014 and 2015, and from an unrelated experiment (that tested for impacts of *Ulva* on *Zostera*, see Chapter 3) in late 2015. *Diloma* and *Micrelenchus* were collected from the same cores at the same time and sites so that possible differences in epibiota communities should mainly be caused by species and shell-size differences, rather than external environmental conditions. Snails were brought back to the lab and stored frozen at -20°C. Defrosted snail shells were measured from bottom of opening to top of spire and examined for any visible (>1 mm) epibiotic organisms under a stereoscope (2014 and early 2015 samples, approximately 4300 snails) or by eye (mid-late

2015 samples, approximately 9,200 snails). Solitary organisms were counted (such as *Ulva* recruits or limpets), while colonial encrusting species, like the bryozoan *Conopeum* spp. and the brown seaweed *Ralfsia* spp. were recorded as present/absent. Analysis of covariance (ANCOVA), with snail size as a covariate factor, tested for differences in epibiont abundance and richness between snail taxa and examination method (stereoscope or naked eye). Variance assumptions and post-hoc analyses were performed as described for the spatial survey.

Results

Distribution

Spatial survey

In the spatial survey, 58% (221) of all samples did not contain any *Micrelenchus* and *Diloma*. Spearman's Rank correlation analysis showed a weak but significant positive relationship between the two snail densities (rho = 0.123, p = 0.016, Figure 6.2), and therefore independence of the two snail taxa could not be assumed. Densities of the two taxa were analysed with two separate ANOVAs. Densities of *Diloma* (log 10 +1 transformed) varied across regions ($p < 0.001$) depending on the presence/absence of seaweed (Region × SW, p = 0.029, Table 6.1A). The northern region had the highest *Diloma* densities in the presence of seaweed (182.6 ± 28.1 m^{-2}), followed by the central region (39.3 ± 30.4 m^{-2}), and the southern region (27.8 ± 9.6 m^{-2}, Figure 6.3A). Densities were also affected by Estuary ($p < 0.001$) depending on the presence of both seagrass and seaweeds (Estuary × SG × SW, p = 0.034) as well as on tidal elevation (Estuary × Elevation, p = 0.019, Table 1A, Figure 6.3B). Puponga had the highest density of *Diloma* (441.6 ± 95.0 m^{-2}), while this species was absent from Dowlings Bay, Duvauchelle Bay, and New River Estuary (Table 6.1A, Figure 6.3A, B). There was also an interaction between tidal elevation and presence of seagrass (Elevation × SG, p = 0.024) showing that *Diloma* was more abundant in the absence of seagrass both in the intertidal (Intertidal: +SG 91.1 ± 20.8 m^{-2}, -SG 106.9 ± 25.9 m^{-2}) and in the subtidal zone (Subtidal: +SG 51.9 ± 12.1 m^{-2}, -SG 80.2 ± 18.8 m^{-2}).

Densities of *Micrelenchus* (log 10 +1 transformed) were also strongly affected by Region ($p < 0.001$), although effects varied by presence of seagrass and seaweeds (Region × SG × SW, p = 0.033, Region × SW, $p < 0.001$, Figure 6.3C), as well as tidal elevation (Region × Elevation, p = 0.028, Table 6.1B, Figure 6.3D). The central region had highest densities

(1482.1 ± 472.5 m^{-2}), followed by the northern region (285.7 ± 45.7 m^{-2}), and the southern region (33.2 ± 10.9 m^{-2}, Figure 6.3C, D). Densities of *Micrelenchus* also differed between estuaries ($p < 0.001$) with several complex interactions with tidal elevations, seagrass, and seaweeds, including a significant Estuary × Elevation × SG × SW four-way interaction ($p = 0.018$, Table 1B, Figure 6.3C, D). *Micrelenchus* had highest densities in the Avon-Heathcote Estuary (4145.9 ± 1204.9 m^{-2}) but was not found in any samples from Jacobs River Estuary, New River Estuary, Ngakuta Bay, or Ruataniwha Inlet (Figure 6.3C, D).

Seasonal survey

In the temporal survey only 14% (36) of the collected cores did not contain any *Micrelenchus* or *Diloma*. Spearman's Rank correlation between *Micrelenchus* and *Diloma* densities was not significant (rho = -0.014, $p = 0.816$), showing independence between the two taxa at this scale. Snail taxa was therefore added as an orthogonal ANOVA test-factor (Figure 6.4). *Micrelenchus* always had higher densities than *Diloma* (3297.1 ± 270.9 vs. 125.5 ± 15.8 m^{-2}, $p < 0.001$) although the magnitude of difference varied across season (Taxa × Season, $p < 0.001$), tidal elevation (Taxa × Elevation, $p < 0.001$), presence of seagrass (Taxa × SG, $p < 0.001$), and presence of seaweed (Taxa × SW, $p < 0.001$), along with higher order interactions of these factors (Table 6.2, Figure 6.5). Generally, densities of *Diloma* were higher in summer (182.1 ± 25.4 m^{-2}) compared to winter (69.3 ± 17.7 m^{-2}), whereas *Micrelenchus* were almost three times more abundant in winter (4873.9 ± 459.5 m^{-2}) than summer (1707.8 ± 205.8 m^{-2}, Figure 6.5A). *Diloma* was more abundant in the intertidal, whereas *Micrelenchus* was more abundant in the subtidal (Figure 6.5C). Both *Diloma* and *Micrelenchus* had higher densities in the presence of seaweed (179.8 ± 28.2 vs. 5428.5 ± 450.2 m^{-2} respectively) than without seaweed (72.5 ± 13.4 vs. 1215.7 ± 160.0 m^{-2}, respectively, Figure 6.5D). Finally, I found that *Micrelenchus* densities were higher in the presence of seagrass (4399.9 ± 406.9 vs. 2167.9 ± 328.5 m^{-2}), whereas *Diloma* was more abundant in the absence of seagrass (147.1 ± 22.8 vs. 104.4 ± 21.9 m^{-2}, Figure 6.5D).

Top-down grazing effects

Laboratory no-choice experiment

Grazing rates were significantly affected by interactions of Taxa × Abundance ($p < 0.001$), Food × Abundance ($p = 0.003$), and Taxa × Food ($p < 0.001$, Table 6.3A). More specifically,

Micrelenchus had the highest grazing rates in both 10 snail (-0.330 ± 0.006, all rates reported per 10 days) and 2 snail additions (-0.006 ± 0.003), compared to *Diloma*, for which the seaweeds gained biomass in the 2 snail addition (+10: -0.002 ± 0.002, +2: 0.001 ± 0.002), and the controls (>0.0001 ± 0.001, Figure 6.6A). Of the seaweeds, *Gracilaria* was the most heavily grazed with 10 snails (g = -0.030 ± 0.006,) followed by *Ulva* with 10 snails (-0.020 ± 0.008), and then *Gracilaria* with 2 snails (-0.007 ± 0.002, Figure 6.6A). Furthermore, *Micrelenchus* had higher grazing rates than *Diloma* in *Gracilaria* additions (-0.028 ± 0.007 vs. -0.009 ± 0.003), *Ulva* additions (-0.027 ± 0.003 vs. 0.006 ± 0.003), as well as *Zostera* additions (-0.004 ± 0.002 vs. 0.001 ± 0.001, Figure 6.6A, Table 6.3A, Figure 6.6A). By comparison, *Diloma* had only a minor grazing effect in high abundances (-0.002 ± 0.002) and a very small positive effect at low abundances (0.001 ± 0.002) and there was no change in seaweed biomass in the control, (i.e., g = 0.000 ± 0.001, Figure 6.6A).

Laboratory choice experiment

As in the no-choice experiment, snail grazing rates were affected by food type ($p = 0.003$), although effects varied between the two snail species (Taxa × Food, $p = 0.002$, Taxa, $p < 0.001$). There was no effect due to the addition of sediments (Sediment, $p = 0.595$, Table 6.3B, Figure 6.6B). *Gracilaria* was grazed significantly more than *Ulva* when snails were given a choice (U+G (G), g = -0.019 ± 0.007, all rates reported per 10 days) and was also heavily grazed in the no-choice treatment (*Gracilaria*, -0.014 ± 0.005, Figure 6.6B). By comparison, snails grazed *Ulva* significantly more in the no-choice treatment (*Ulva*, -0.009 ± 0.007) than when *Ulva* co-occurred with *Gracilaria* (U+G (U), 0.0001 ± 0.001, Figure 6.6B). Finally, *Micrelenchus* had, again, significantly higher grazing rates (-0.030 ± 0.006) than *Diloma* (-0.001 ± 0.001, the latter was no different from the no-grazer control cages; 0.000 ± 0.001, $p = 0.975$, Figure 6.6B).

Field experiment of grazing rates of Micrelenchus

In the field experiment, grazing rates were affected by the Food × Snail interaction ($p < 0.001$), food type ($p < 0.001$), and, not surprisingly, by the presence of snails ($p < 0.001$, Table 6.3C). Grazing rates were significantly higher on *Gracilaria* in the no-choice treatment (g = -0.067 ± 0.023, rates reported per 10 days), followed by *Gracilaria* in the choice treatment (-0.042 ± 0.015[1]), *Ulva* alone (-0.019 ± 0.007), and *Ulva* in the choice treatment (-

0.004 ± 0.003, Figure 6.6C, but there was no difference in *g* between *Ulva* only and *Ulva* in the choice treatment, p = 0.076). Overall, grazing rates of *Micrelenchus* (-0.066 ± 0.011) was also significantly higher than the controls (0.000 ± 0.002, Figure 6.6C).

Bottom-up habitat provision

The collected *Diloma* had an average height of 7.88 ± 0.09 mm, while *Micrelenchus* had an average height of 5.79 ± 0.02 mm (Table 4). However, even though *Diloma* had larger shells, a higher proportion of *Micrelenchus* shells provided habitat to at least one epibiont (57 vs. 43% respectively, Table 4). *Diloma* shells were inhabited by more *Ulva* and barnacles whereas *Micrelenchus* supported more *Gigartina* and *Ralfsia* (Table 4). Size distributions of *Diloma* followed a bimodal pattern with most snails being 4 or 10 mm long (*n* = 153 and 160, respectively, Figure 6.7A). The smallest snails (<2 mm) were inhabited by fewest epibionts, intermediate shell sizes had relatively high levels of epibionts (peaking between 9-13 mm), and larger snails (14-17mm), relatively low levels of epibionts. The size distribution of *Micrelenchus* was unimodal with most snails being 6 mm long (*n* = 3840) and only 3 snails were larger than 11 cm (Figure 6.7D). Small shells had, again, fewest epibionts (<5 mm = <20% occupancy) whereas all larger shells had at least 40% occupancy of epibionts. More specifically, a single collected 14 mm *Micrelenchus* was inhabited by epibionts (i.e., 100%) whereas 7- and 10-mm long shells had the second highest proportion of snails with epibionts (ca. 85%, Figure 6.7D).

As hypothesized, the abundance of epibionts on *Diloma* (3.37 ± 0.57) was significantly higher than on *Micrelenchus* (1.39 ± 0.07) (Taxa, p = 0.008, see Table 6.5A), regardless of methodology (Size × Taxa × Method, p = 0.103, Taxa × Method, p = 0.381, Table 6.5A), where abundances generally increased with snail size up to a certain point (Size × Taxa, p < 0.001; Size, p < 0.001, Table 6.5A, Figure 6.7B). Abundance of epibionts was also significantly higher when counted under the microscope (3.74 ± 0.27) compared to without a microscope (0.61 ± 0.01) (Method, p < 0.001) again co-varying with shell size (Size × Method, p = 0.029, Table 6.5A). Epibiont richness had complex higher-order significant interactions between snail sizes, taxa and methodology (Size × Taxa × Method = p < 0.001, Taxa × Method = p < 0.001, Size × Type = p < 0.001, and Size × Taxa = p < 0.001)). *Micrelenchus* generally had higher epibiont richness per snail (1.26 ± 0.01) than *Diloma* (0.95 ± 0.03, Figure 6.7C, F), and the stereoscope counting method showed higher richness

(1.85 ± 0.02) than counting with the naked eye (1.07 ± 0.01, Table 5; note that variances could not be transformed to homogeneity, so alpha was reduced to 0.01 for this test).

Discussion

Virtually all research about foundation species has focused on sessile species (Ellison et al. 2005, Altieri et al. 2007). In estuaries, seagrasses and seaweeds are generally considered the most important (sessile) foundation species (Orth et al. 1984, Beal 1994, Boström et al. 2006, Gribben and Wright 2006, Thomsen 2010, Thomsen et al. 2012a, Wright et al. 2014), but mobile species such as snails can also play a similar ecological role, providing habitat and mediating trophic transfer of matter and energy (Buschbaum and Reise 1999, Chan and Chan 2005, Wernberg et al. 2010). However, in contrast to sessile foundation species, mobile foundation species can have dual ecological roles by simultaneously creating habitat and exerting top down control through grazing or predation. This study is the first to show that two common estuarine snails, *Diloma nigerrimum* and *Micrelenchus huttonii* and abundant in estuaries across New Zealand, and produce positive effects to communities through habitat provision, and negative effects through grazing, simultaneously.

Distribution

Effects of latitude

My hypothesis that the two trochid snails would have the highest densities in the northern region on the South Island of New Zealand due to the warmer climate (Macara 2016, NIWA 2016), was only partially supported by the results of this study. *Diloma* densities were highest in the northern region, while *Micrelenchus* had the highest densities in the central region. Both *Micrelenchus* and *Diloma* had the lowest densities in estuaries in the southern region. This latitudinal pattern of low density in southern regions may be linked to the thermal limits of the two-species. For example, in the whelk *Kelletia kelletii*, a sharp 3° C ocean surface temperature drop at a single sample location (over a 6° latitudinal range) limited its expansion towards higher latitudes (Zacherl et al. 2003). I observed a similar latitudinal pattern (Figure 1), with lower snail densities towards the higher latitudes, thus temperature could play a role in the distributions of the two snails. However, I could not test this as water temperature was not recorded during collections. Between the northern and southern regions on the South Island, there is a distinct gradient in climate, although there is only a ca. 6° latitudinal

difference. For example, in the northern region, 2016 annual mean temperature in Nelson was 13.8°C (NIWA 2016) and had 2400 hours of sunlight (Macara 2016), while in the southern region, Invercargill had a mean annual temperature of 10.9°C (NIWA 2016) and 1600 hours of sunlight (Macara 2016). This decrease in species abundance and richness towards the higher latitudes in New Zealand has also been found in fish (McClatchie et al. 1997, Francis et al. 2011) and crabs (Jones and Simons 1983).

My hypothesis that *Micrelenchus* would be more abundant than *Diloma* in all sampled estuaries, based on the premise that smaller organisms are usually more abundant (Andersen and Beyer 2006), was rejected. *Micrelenchus* only had higher mean densities than *Diloma* in 8 estuaries out of 15 around the South Island of New Zealand. Although *Micrelenchus* was common around all estuaries (only absent in samples from 4 estuaries), there was one particularly surprising finding of *Micrelenchus* densities in the Avon-Heathcote Estuary. The density in that estuary was several orders of magnitude higher than not only the local *Diloma* densities, but all other snail densities in every sampled estuary as well. The reason for the localized high density of *Micrelenchus* is unclear, but past high-magnitude earthquakes (years 2010 and 2011) altered the benthos of the Avon-Heathcote Estuary (Measures et al. 2011, Zeldis et al. 2011); sewage leaked into the estuary, increasing nutrient inputs (Zeldis et al. 2011), which may have boosted ephemeral seaweed and microalgal populations (Nelson et al. 2015) potentially influencing (as a food source) *Micrelenchus* densities.

Effects of elevation

The hypotheses that *Diloma* would be more abundant in the intertidal zone and *Micrelenchus* in the subtidal zone were rejected. *Diloma* was more abundant in the intertidal only in 6 of the 15 sampled estuaries (and was found in similar quantities between zones in the more detailed seasonal survey in the Avon-Heathcote Estuary). *Micrelenchus* was more abundant in the shallow subtidal zone only in 6 sampled estuaries, including the seasonal survey. These results may be explained by the snail life cycle: for example, in Japan, juveniles of *Diloma suavis* settle at low elevation, but move to higher elevations as they grow larger (Iwasaki 2000), possibly because they become more resistant to desiccation with larger size (Chen and Richardson 1987, Thivakaran and Kasinathan 1990, Edwards 2015). The tidal movement of *Diloma* in different life-stages could be why I found the snail in both tidal zones, and in

similar quantities in the Avon-Heathcote Estuary, unfortunately snail-size was not measured in this study to discern adults from juveniles. However, Miller and Poulin (2001) found larger *Diloma* (likely adults) move greater distances during low-tide than smaller individuals, although parasitic trematode loads can affect this greatly (i.e., parasitized snails move less, and parallel to water, where non-parasitized snails move perpendicular to water). It is also possible that distributions of *Diloma* and *Micrelenchus* are simply controlled by vegetation, such as drifting seaweed and seagrass (see next section), so that elevation effects *per se* are only of minor importance, which may also apply to *Diloma* (see next section).

Effect of habitat

The hypothesis that *Diloma* would be most abundant on bare sediments was also rejected (*Diloma* was more abundant in vegetated habitats). Logan (1976) found that *Diloma subrostratum* was more common on hard substrates like pebbles or rocks than mud, although the snail could move on both types of substrate. Similarly, Thrush et al. (2008) also did not find any *D. subrostratum* in sediments that consisted of mud >12% per 6 cm^3 sediment sample. Logan (1976) also found that *D. subrostratum* preferred not to aggregate around seaweed, and most of their gut contents consisted of sand (Logan 1976), but perhaps *Diloma* use multiple habitats during the day to feed or mitigate stress. As my samples were taken at low tide, *Diloma* could have been using seagrass and seaweeds to buffer environmental stress, hence why they were more abundant in vegetated habitats versus bare sediments as found in many previous studies.

Micrelenchus and other closely-related and co-occurring species (i.e., *Cantharidus dilatatus* and *Micrelenchus tenebrosus*) were found to be more abundant in the presence of seaweed, as well as seagrass, in line with the findings of previous studies (Henriques 1980, Taylor 1997, Grove and Probert 1999, Battley et al. 2011). Seaweeds provide refuge from desiccation and predation and can also be an important food source for the snails (see grazing section below) (Wilson et al. 1990, Geertz-Hansen et al. 1993, Norkko et al. 2000, Thomsen 2010, Thomsen and Wernberg 2015, Ramus et al. 2017).

Effects of season

I found, as initially hypothesized, that *Diloma* was more abundant in summer than winter, probably because of higher food availability in summer (Lavery et al. 1991, Hauxwell et al.

1998). However, a study of another trochid snail from Japan, *Diloma suavis*, found an opposite pattern: snail abundances increased yearly from autumn to winter, and then decreased the following summer, after reproduction had taken place, suggesting a one-year lifespan (Iwasaki 2000). If I use this as a template for New Zealand *Diloma*, it would be likely that the snails hatch and grow in summer, reproduce during winter, and then die after reproduction has taken place. Unfortunately, no studies exist that examine life history and seasonal patterns of *Diloma* spp., especially in New Zealand (Creese 1988). *Micrelenchus*, on the other hand, had higher abundances in winter than summer samples. I expected *Micrelenchus* to have high densities in summer, when the seaweed *Ulva* (that the snail uses for food and habitat) is much more abundant (Chapter 3, Ren et al. 2014). *Ulva* blooms continue into late autumn, with the biomass usually peaking in early autumn (Ren et al. 2014). There may be a lag time between seaweed blooms and the period in which the highest densities of *Micrelenchus* appear in the Avon-Heathcote Estuary. Differences in seasonality of the two snails may also be due to seasonal patterns of recruitment and life-span (Rainer 1981, Holland et al. 1987, Platell and Potter 1996), although no studies have examined the life-history of *Micrelenchus*, and only one has done this for a *Diloma* species in Japan, which indicated that *Diloma suavis* lives for approximately 1 year (Iwasaki 2000). Finally, environmental factors, such as dissolved oxygen and water temperature (Jigyasu and Singh 2009, Palpandi 2011), desiccation stress (Cranford 1988, Vaughn and Fisher 1992), and evolutionary avoidance of predators like migratory birds and fish (Pyron and Covich 2003) may also affect snail seasonality.

Top-down grazing

I found virtually no grazing effect on seagrass, similar to other studies that have tested for an effect of generalist grazers on seagrasses (Kitting et al. 1984, Orth and Van Montfrans 1984, Fredriksen et al. 2004, but see Unabia 2011 for specialist seagrass-grazer taxa). Most marine snails do not consume seagrass itself, in part because a specialized radula is needed to feed on their tough blades (Unabia 2011), and because seagrass do not emit olfactory chemicals that attract snails like many seaweeds do (Brönmark 1985, Fink et al. 2006). Instead, the algal epiphytes and periphyton growing on seagrass leaves are typically grazed (Kitting et al. 1984, Orth and Van Montfrans 1984, Brönmark 1989, Klumpp et al. 1992, Hily et al. 2004, Gacia et al. 2009, Holzer et al. 2011). In contrast, both the green seaweed *Ulva* and red seaweed *Gracilaria* were grazed upon by both snails. *Ulva* is a thin fast-growing seaweed that can

generate large amounts of biomass quickly (Raffaelli et al. 1998, Nelson et al. 2003), often 'outgrowing' grazing pressures, whereas *Gracilaria* is a branched, red seaweed that inhabit a few patchy areas in the Avon-Heathcote Estuary, and does not seem to create large seasonal blooms (Hollever and Bolton-Ritchie 2016). Interestingly, *Gracilaria* was grazed more heavily (both with and without sediments) than *Ulva*. Indeed, the high snail treatments (ca. 260 snails m^{-2}; slightly higher than typical *Diloma* densities, but much lower than typical *Micrelenchus* densities in the Avon-Heathcote) showed major grazing effects of *Micrelenchus*, but not *Diloma*, in all experiments. This result suggests that *Gracilaria* could potentially be top-down controlled by *Micrelenchus* grazing in the Avon-Heathcote Estuary, although actual biomass of *Gracilaria* in the field would have to be measured, to truly see if this is possible. This high grazing rate of *Gracilaria* contrasts with many other studies that suggest that seaweed is typically a poor food source (Granado and Caballero 1991, Thomsen and McGlathery 2007, Araújo et al. 2015). The differential effects between the two snail species could potentially be associated with different radulas with *Micrelenchus* grazing on macroalgae (Henriques 1980, Taylor 1997, Battley et al. 2011, Thomsen et al. 2016) and *Diloma* consuming biofilms and microalgae on sand particles (Logan 1976, Iwasaki 2000), although it can also feed on some seaweed (this study).

Bottom-up habitat provision

Typically, snails with large shells host more abundant and diverse communities of epibionts than animals with small shells (Vasconcelos et al. 2007, Wernberg et al. 2010, Thyrring et al. 2013), as would be expected from simple species-area relationships (Simberloff 1976, Aho 1978). My results supported these findings, as small trochid snails had the least epibiota, even if very large shells also had low epibiont abundances (Figure 6.7). Low epibiont abundance (particularly small *Ulva* recruits) on the largest shells could be caused by top-down grazing effects, for example from epibiotic limpets (like *Notoacmea* spp.). Similar top-down control of epibiota can occur on large trochid shells in kelp beds in Australia (Wernberg et al. 2010), on large pen shells in seagrass beds (Gribben et al. 2017), and on coral reefs (Coen 1988, Sazima et al. 2010). There could also be other factors necessary for epibionts to grow other than suitable surface area, such as shell-conditioning (predators or environment creating gouges and rough areas for epibionts to settle in; (Schmitt et al. 1983), weakened antifouling defences of the snails from parasites, allowing colonization (Wahl 1989, Wahl and

Sönnichsen 1992, Mouritsen 2017), or a combination of both shell-conditioning and parasitic load (Thieltges and Buschbaum 2007).

Although subtle, there are ecological and morphological differences between *Diloma* and *Micrelenchus*. *Micrelenchus* is smaller, has a ridged shell, and prefers vegetated habitats such as seaweed and seagrass (Henriques 1980, Taylor 1997, Battley et al. 2011), whereas *Diloma* can grow to larger sizes, has a smoother shell, and appears to be less selective in its habitat preference, which may be due to its feeding preferences and/or stress adaptations (Logan 1976, Mitchell 1980, Iwasaki 2000). Unfortunately, very few studies have been conducted on these two specific snails and the longevity of these snails is unknown. I found that *Micrelenchus* hosted more algal epibionts (*Ulva*, *Porphyra*, *Sarcothalia*, *Gelidium*) as well as encrusting epibiota (Bryozoa, *Ralfsia*) than *Diloma* (Table 6.4). The higher epibiota load may be caused by *Micrelenchus'* association with seaweed and seagrass habitats where stress from desiccation and predation/grazing are likely lowered (Norkko 1998, Norkko et al. 2000, Cardoso et al. 2004, Thomsen 2010), thereby increasing survival of small algal recruits and encrusting organisms. Some species of seaweeds such as *Ulva* can reproduce asexually, by sloughing cells or fragmentation of the main blade (Bonneau 1978, Zhang et al. 2016). Thomsen et al. (2010b), also found high fragmentation production when epiphytic seaweeds were densely packed on snail shells. These types of recruitment may help to explain the abundance of *Ulva* on snail shells seen here, especially *Micrelenchus* as they are regularly in contact with *Ulva* biomass in their daily behaviours and had high densities of epiphytic *Ulva*. Between the two examination methods, I found more epibionts under the microscope than by the naked eye alone, mainly because I counted many more small *Ulva* recruits under the scope. Although I counted more epibionts under the stereoscope, this method requires shells to be brought to the laboratory and it is order of magnitudes slower, and thereby reduces the number of replicates that can be processed in a given time.

Conclusions

I found that two co-occurring morphologically similar estuarine snails, *Micrelenchus huttonii* and *Diloma nigerrimum*, were common in most sampled estuaries on the South Island of New Zealand, provided positive effects to communities through habitat creation, and negative effects through grazing. Overall, *Diloma* was found in more estuaries, *Micrelenchus* could reach higher maximum densities, *Micrelenchus* was relatively more abundant in winter, and both species were more abundant in seaweed habitats where they likely experience reduced

desiccation and predation and find more food. I also found that *Micrelenchus* had much stronger grazing effects on seaweeds compared to *Diloma*, and *Micrelenchus* may even exert top-down control of *Gracilaria*, a result that have not been shown before. Finally, I found that *Micrelenchus* were inhabited by more sessile epibionts than *Diloma*, although abundances of *Ulva* recruits were higher on *Diloma* shells. This study shows that small mobile organisms can be important foundation species both as grazers and as habitat-providers, and should not be overlooked in research, conservation or restoration of estuarine and coastal environments.

Tables

Table 6.1 ANOVA tables of densities of (A) *Diloma nigerrimum* (log 10 +1 transformed), and (B) *Micrelenchus huttonii* (log 10 +1 transformed), from a latitudinal survey of 15 estuaries from 3 regions (North, Central, South) on the South Island of New Zealand. Additional orthogonal test factors included tidal elevation (intertidal vs. subtidal), presence and absence of seagrass (± SG) and presence and absence of seaweed (± SW). Densities of *Diloma* and *Micrelenchus* were correlated (see Figure 3) so separate analyses were done for the two taxa. Significant effects are in bold.

Species	Test Factor	Df	SS	F-value	p
(A) Diloma	**Region**	**2**	**63.75**	**44.965**	**<0.001**
	Estuary	**12**	**65.19**	**7.663**	**<0.001**
	Elevation	1	0.83	1.175	0.279
	Seagrass (SG)	1	1.07	1.516	0.219
	Seaweed (SW)	**1**	**3.74**	**5.274**	**0.022**
	Region×Elevation	2	0.60	0.426	0.654
	Estuary×Elevation	**12**	**17.60**	**2.069**	**0.019**
	Region×SG	2	3.02	2.132	0.121
	Estuary×SG	12	12.16	1.430	0.152
	Elevation×SG	**1**	**3.65**	**5.149**	**0.024**
	Region×SW	**2**	**5.10**	**3.598**	**0.029**
	Estuary×SW	12	12.56	1.477	0.133
	Elevation×SW	1	0.61	0.854	0.356
	SG×SW	1	0.11	0.154	0.695
	Region×Elevation×SG	2	0.30	0.214	0.808
	Estuary×Elevation×SG	12	10.24	1.204	0.280
	Region×Elevation×SW	2	2.01	1.417	0.244
	Estuary×Elevation×SW	11	7.12	0.913	0.528
	Region×SG×SW	2	0.44	0.308	0.735
	Estuary×SG×SW	**10**	**14.13**	**1.993**	**0.034**
	Elevation×SG×SW	1	0.52	0.738	0.391
	Region×Elevation×SG×SW	2	3.54	2.496	0.084
	Estuary×Elevation×SG×SW	8	5.49	0.969	0.461
	Residuals	267	189.27		
(B) Micrelenchus	**Region**	**2**	**76.59**	**78.664**	**<0.001**
	Estuary	**12**	**189.66**	**32.464**	**<0.001**
	Elevation	**1**	**2.38**	**4.898**	**0.028**
	Seagrass (SG)	**1**	**13.82**	**28.381**	**<0.001**
	Seaweed (SW)	**1**	**22.84**	**46.921**	**<0.001**
	Region×Elevation	**2**	**11.75**	**12.071**	**<0.001**
	Estuary×Elevation	**12**	**23.11**	**3.956**	**<0.001**
	Region×SG	2	1.73	1.776	0.171
	Estuary×SG	**12**	**19.66**	**3.365**	**<0.001**
	Elevation×SG	**1**	**2.40**	**4.938**	**0.027**
	Region×SW	**2**	**11.36**	**11.664**	**<0.001**
	Estuary×SW	**12**	**24.13**	**4.131**	**<0.001**

Elevation×SW	1	1.14	2.340	0.127
SG×SW	**1**	**2.61**	**5.370**	**0.021**
Region×Elevation×SG	2	1.41	1.446	0.237
Estuary×Elevation×SG	**12**	**20.90**	**3.578**	**<0.001**
Region×Elevation×SW	2	0.66	0.673	0.511
Estuary×Elevation×SW	11	6.27	1.171	0.307
Region×SG×SW	**2**	**3.37**	**3.463**	**0.033**
Estuary×SG×SW	10	7.03	1.444	0.161
Elevation×SG×SW	1	0.91	1.862	0.174
Region×Elevation×SG×SW	2	1.11	1.140	0.322
Estuary×Elevation×SG×SW	**8**	**9.19**	**2.359**	**0.018**
Residuals	267	129.99		

Table 6.2 ANOVA table of snail densities found from a temporal survey in the Avon-Heathcote Estuary over two years. Examined orthogonal test factors include snail taxa (*Diloma nigerrimum* and *Micrelenchus huttonii*), seasons (summer, winter), sites (Plover St. closer to river mouth, vs. Tern St. closer to ocean entrance), tidal elevations (intertidal vs. subtidal), presence or absence of seagrass (± SG) and presence or absence of seaweed (± SW). Alpha was reduced to 0.01 for this test because of variance heterogeneity. Densities of *Diloma* and *Micrelenchus* were not correlated (see Figure 5), so Taxa was added as an orthogonal test factor. Significant effects are in bold.

	Df	SS	F-value	p
Taxa	**1**	**1272000000**	**309.475**	**<0.001**
Season	**1**	**294800000**	**71.702**	**<0.001**
Site	1	190700	0.046	0.830
Elevation	**1**	**61620000**	**14.987**	**<0.001**
SG	**1**	**150800000**	**36.679**	**<0.001**
SW	**1**	**584600000**	**142.189**	**<0.001**
Taxa×Season	**1**	**340000000**	**82.692**	**<0.001**
Taxa×Site	1	762800	0.186	0.667
Season×Site	1	13600000	3.307	0.070
Taxa×Elevation	**1**	**68290000**	**16.609**	**<0.001**
Season×Elevation	1	1762000	0.429	0.513
Site×Elevation	1	18430000	4.483	0.035
Taxa×SG	**1**	**162700000**	**39.575**	**<0.001**
Season×SG	1	4139000	1.007	0.316
Site×SG	1	3476000	0.845	0.358
Elevation×SG	1	4700000	1.143	0.286
Taxa×SW	**1**	**527700000**	**128.332**	**<0.001**
Season×SW	**1**	**144900000**	**35.235**	**<0.001**
Site×SW	1	958500	0.233	0.629
Elevation×SW	1	10630000	2.584	0.109
SG×SW	1	294700	0.072	0.789
Taxa×Season×Site	1	17550000	4.268	0.039
Taxa×Season×Elevation	1	2480000	0.603	0.438
Taxa×Site×Elevation	1	17420000	4.237	0.040
Season×Site×Elevation	**1**	**33470000**	**8.141**	**0.005**
Taxa×Season×SG	1	6591000	1.603	0.206
Taxa×Site×SG	1	4788000	1.165	0.281
Season×Site×SG	1	7659000	1.863	0.173
Taxa×Elevation×SG	1	8178000	1.989	0.159
Season×Elevation×SG	1	1673000	0.407	0.524
Site×Elevation×SG	1	5909000	1.437	0.231
Taxa×Season×SW	**1**	**162100000**	**39.423**	**<0.001**
Taxa×Site×SW	1	760100	0.185	0.667
Season×Site×SW	1	11120000	2.704	0.101
Taxa×Elevation×SW	1	14770000	3.593	0.059
Season×Elevation×SW	1	509	0.000	0.991
Site×Elevation×SW	1	13640000	3.316	0.069

Taxa×SG×SW	1	539000	0.131	0.717
Season×SG×SW	1	5311000	1.292	0.256
Site×SG×SW	1	117200	0.028	0.866
Elevation×SG×SW	1	429200	0.104	0.747
Taxa×Season×Site×Elevation	**1**	**31840000**	**7.744**	**0.006**
Taxa×Season×Site×SG	1	9831000	2.391	0.123
Taxa×Season×Elevation×SG	1	4350000	1.058	0.304
Taxa×Site×Elevation×SG	1	4292000	1.044	0.308
Season×Site×Elevation×SG	1	1179000	0.287	0.593
Taxa×Season×Site×SW	1	14380000	3.497	0.062
Taxa×Season×Elevation×SW	1	10230	0.002	0.960
Taxa×Site×Elevation×SW	1	15990000	3.888	0.049
Season×Site×Elevation×SW	1	21880000	5.320	0.022
Taxa×Season×SG×SW	1	3936000	0.957	0.328
Taxa×Site×SG×SW	1	171100	0.042	0.838
Season×Site×SG×SW	1	5393000	1.312	0.253
Taxa×Elevation×SG×SW	1	659000	0.160	0.689
Season×Elevation×SG×SW	1	5420000	1.318	0.252
Site×Elevation×SG×SW	1	8149000	1.982	0.160
Taxa×Season×Site×Elevation×SG	1	767500	0.187	0.666
Taxa×Season×Site×Elevation×SW	1	16410000	3.990	0.046
Taxa×Season×Site×SG×SW	1	8749000	2.128	0.145
Taxa×Season×Elevation×SG×SW	1	8346000	2.030	0.155
Taxa×Site×Elevation×SG×SW	1	6723000	1.635	0.202
Season×Site×Elevation×SG×SW	1	433000	0.105	0.746
Taxa×Season×Site×Elevation×SG×SW	1	669600	0.163	0.687
Residuals	442	1817000000		

Table 6.3 ANOVA table examining grazing rates in various experiments in (A) Laboratory with no-choice of food (either *Zostera, Gracilaria,* or *Ulva*), for *Diloma nigerrimum* and *Micrelenchus huttonii* (taxa) in two abundances 2 or 10 snails, plus control. (B) Laboratory experiment with food choice (*Ulva*, *Gracilaria*, or *Ulva+Gracilaria*), with +/- 2 cm of sediment added for 10 snails of *Diloma* and *Micrelenchus*. Alpha was reduced to 0.01 for this test as variance homogeneity could not be confirmed. (C) Field experiment with food choice (*Ulva*, *Gracilaria*, or *Ulva+Gracilaria*) for 10 *Micrelenchus* snails.

Exp. Type	Test Factor	Df	SS	F-value	p
(A) Lab No-Choice	**Taxa**	**2**	**0.0081**	**34.944**	**<0.001**
	Food	**2**	**0.0028**	**11.944**	**<0.001**
	Abundance	**1**	**0.004**	**34.243**	**<0.001**
	Taxa×Food	**4**	**0.0031**	**6.737**	**<0.001**
	Food×Abundance	**2**	**0.0014**	**6.189**	**0.003**
	Taxa×Abundance	**1**	**0.0024**	**21.032**	**<0.001**
	Taxa×Food×Abundance	2	0.0005	2.329	0.104
	Residuals	75	0.0087		
(B) Lab Choice	**Taxa**	**2**	**0.0286**	**30.821**	**<0.001**
	Food	**3**	**0.0069**	**4.977**	**0.003**
	Sediment (Sed)	1	0.0001	0.285	0.595
	Food×Sed	3	0.0005	0.326	0.806
	Taxa×Food	**6**	**0.0106**	**3.789**	**0.002**
	Taxa×Sed	2	0.0006	0.673	0.512
	Taxa×Food×Sed	6	0.0004	0.139	0.991
	Residuals	120	0.0557		
(C) Field Choice	**Taxa**	**1**	**0.0434**	**256.48**	**<0.001**
	Food	**3**	**0.0226**	**44.51**	**<0.001**
	Taxa×Food	**3**	**0.0226**	**44.51**	**<0.001**
	Residuals	32	0.0054		

Table 6.4 Mean (± SE) length (mm) and epibiont abundances (per shell) attached to the trochid snails *Diloma nigerrimum* (*n*=1543, 661 snails with at least one epibiont) and *Micrelenchus huttonii* (*n*=11939, 6751 snails with at least one epibiont) in the Avon-Heathcote Estuary. Total = number of shells inhabited by a specific epibiont. * = calculated from presence-absence only.

	Diloma		***Micrelenchus***	
	Mean±SE	Total	Mean±SE	Total
Length	7.88±0.09	1543	5.79±0.02	11939
Ulva	3.17±0.57	4898	0.87±0.07	10398
Porphyra	0.01±0.005	22	0.01±0.001	73
Barnacles	0.01±0.004	15	0.002±0.001	22
Sarcothalia	0.001±0.001	1	0.006±0.001	72
Gelidium	0.001±0.001	1	0.001±0.001	15
Ralfsia*	**16.1%**	248	**48.4%**	5776
Bryozoa*	**0.97%**	15	**1.9%**	226

Table 6.5 Two-way ANCOVA table, with Size as a covarying factor, examining (A) epibiont abundance and (B) epibiont taxa richness found on two snail taxa (*Diloma nigerrimum* and *Micrelenchus huttonii*), and two examination methods (stereoscope and naked eye). Alpha was reduced to 0.01 for both tests as variance homogeneity could not be confirmed even after attempted transformations. Significant effects are in bold.

Measure	Test factor	Df	SS	F-value	p
(A) Abundance	**Taxa**	**1**	**693**	**6.98**	**0.008**
	Size (covariate)	**1**	**23323**	**235.02**	**<0.001**
	Method	**1**	**15777**	**158.98**	**<0.001**
	Taxa×Size	**1**	**1759**	**17.72**	**<0.001**
	Size×Method	1	472	4.75	0.029
	Taxa×Method	1	76	0.77	0.381
	Taxa×Size×Method	1	264	2.66	0.103
	Residuals	13474	1337134		
(B) Richness	**Taxa**	**1**	**946**	**1128.49**	**<0.001**
	Size (covariate)	**1**	**3085**	**3678.75**	**<0.001**
	Method	**1**	**464**	**553.39**	**<0.001**
	Taxa×Size	**1**	**1386**	**1653.11**	**<0.001**
	Size×Method	**1**	**713**	**849.78**	**<0.001**
	Taxa×Method	**1**	**17**	**20.17**	**<0.001**
	Taxa×Size×Method	**1**	**115**	**137.19**	**<0.001**
	Residuals	13474	11298		

Figures

Figure 6.1 (A) Map of 15 sampled estuaries on the South Island of New Zealand divided into a northern (estuary A-F), central (G-H) and southern (J-M) region. (B) Morphology of the two trochid snails *Diloma nigerrimum* and (C) *Micrelenchus huttonii*. *Diloma* is typically wider than tall in a depressed-globose shell shape, and usually found on sediments and hard substrates in low, mid, and high tide zones (Jones et al. 2005). The maximum height of *Diloma* is 24 mm (Powell 1979). *Micrelenchus* is smaller (maximum height of 15 mm) (Marshall 1998) and the shell is taller than wide in a conico-turbinate shape and are usually found on seaweed or seagrass in the low to mid tide zones (Jones et al. 2005). Note that drawings are not to scale.

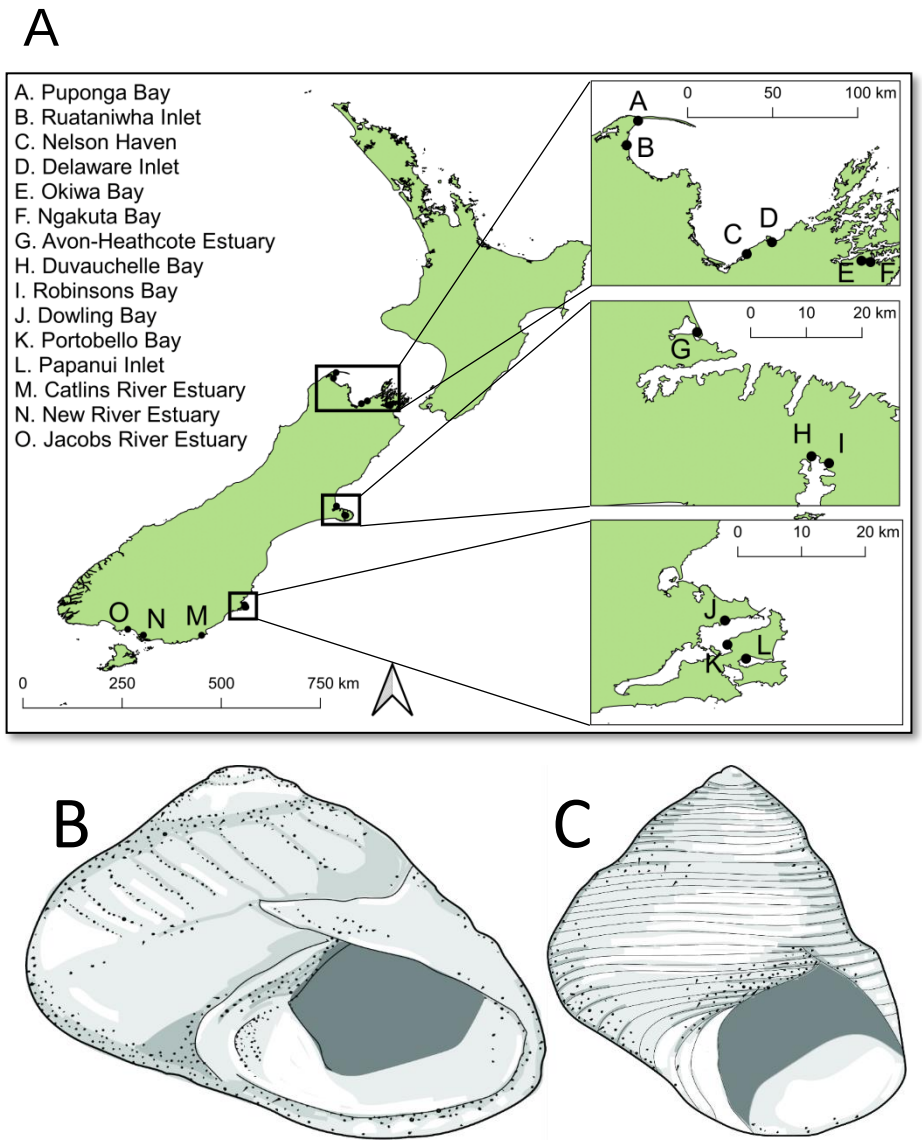


Figure 6.2 Densities of *Micrelenchus huttonii* vs. *Diloma nigerrimum* in 15 estuaries on the South Island of New Zealand. There was a weak significant positive relationship between the two snail taxa. White symbols represent northern estuaries, grey symbols are central estuaries, and black symbols are southern estuaries. There were 221 samples (58% of all collected cores) without any *Micrelenchus* or *Diloma*.

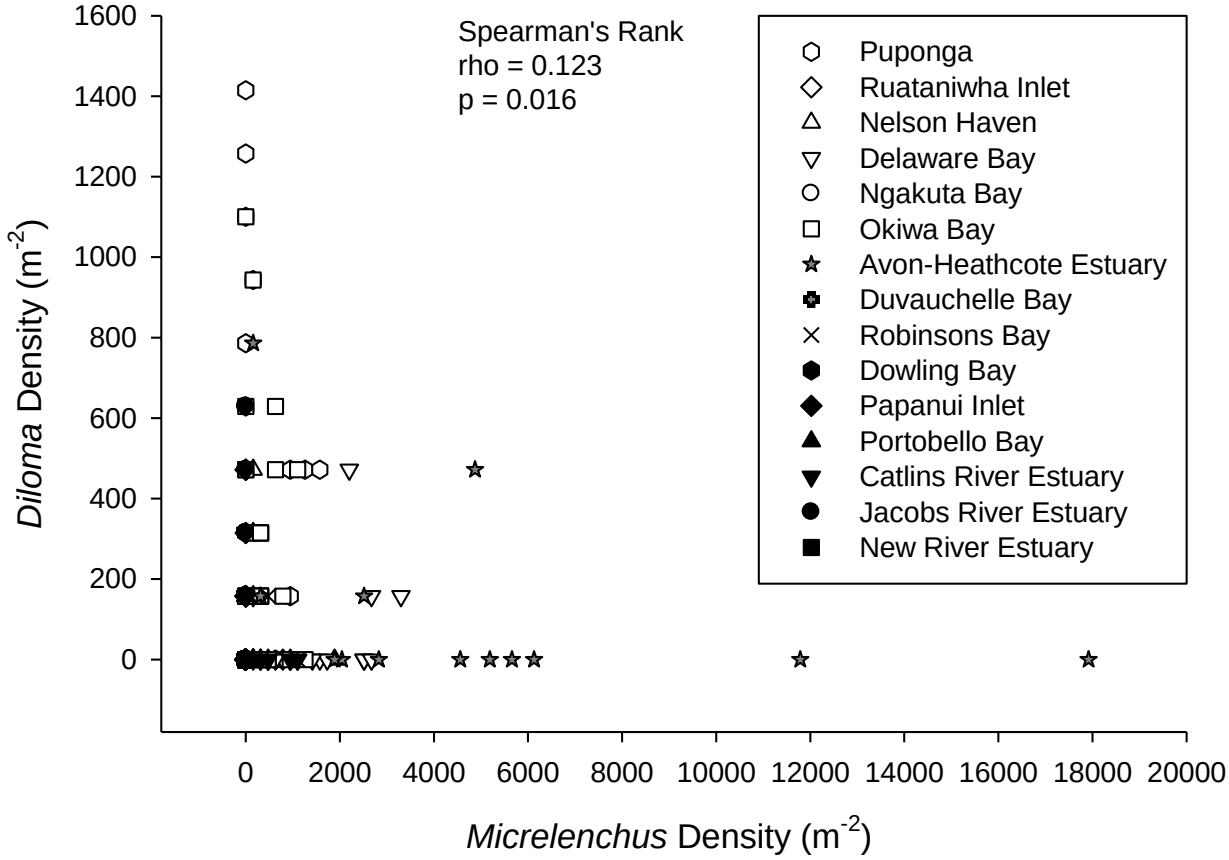


Figure 6.3 Mean densities (+SE) of the trochid snails *Diloma nigerrimum* (A, B) and *Micrelenchus huttonii* (C, D) in four habitat types (A, C) and two tidal elevations (B, D) from 15 estuaries around the South Island of New Zealand. Samples were collected by benthic cylindrical cores, 9 cm diameter × 10 cm depth. Dashed lines show estuaries classified by latitudinal region, SG = Seagrass.

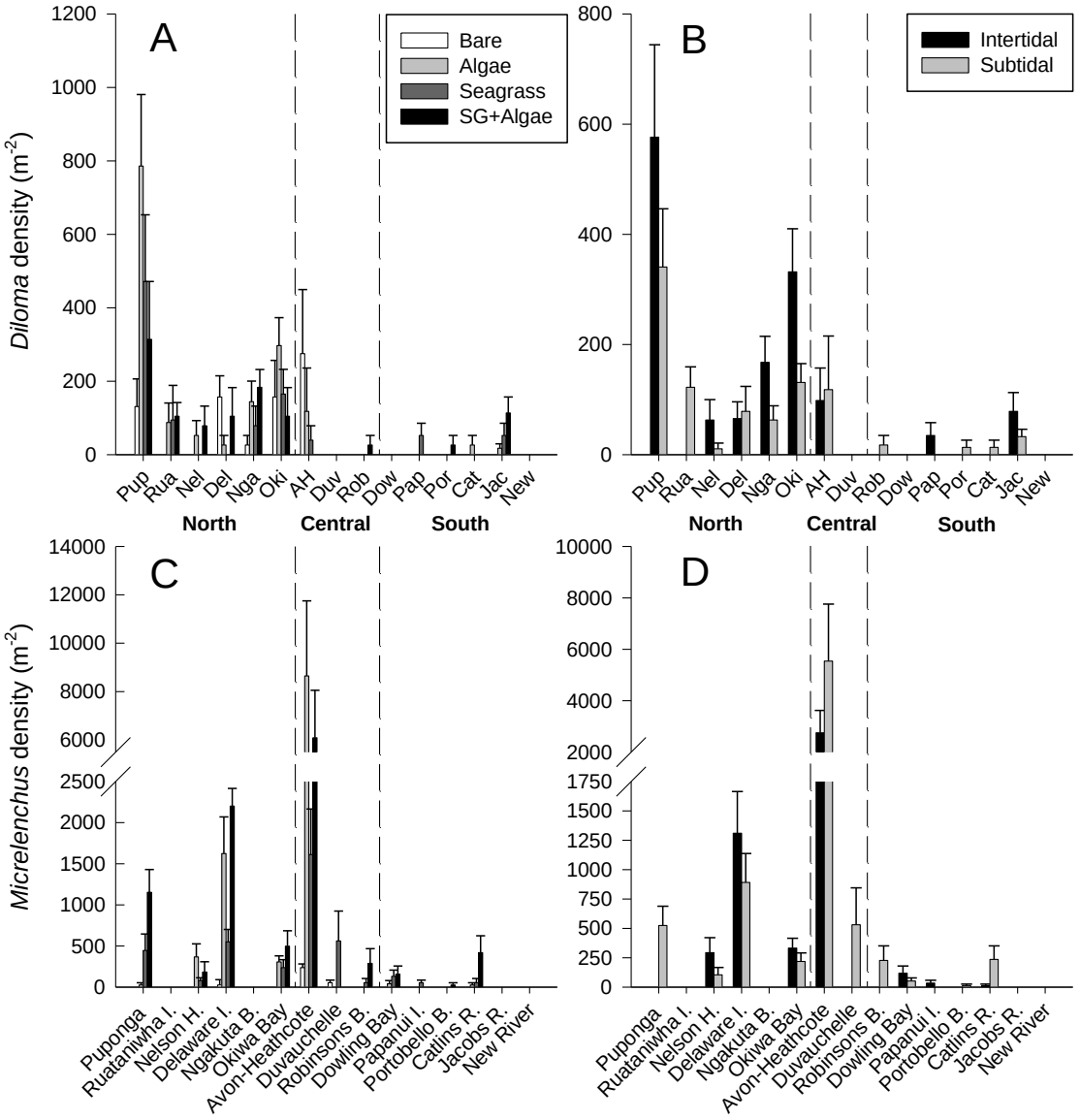


Figure 6.4 Densities of *Micrelenchus huttonii* vs. *Diloma nigerrimum* in four different habitats in the Avon-Heathcote Estuary. There was no significant relationship between the two snail taxa. Black and white symbols represent summer and winter samples, respectively. There were 36 samples (14% of collected cores) without any *Micrelenchus* or *Diloma*.

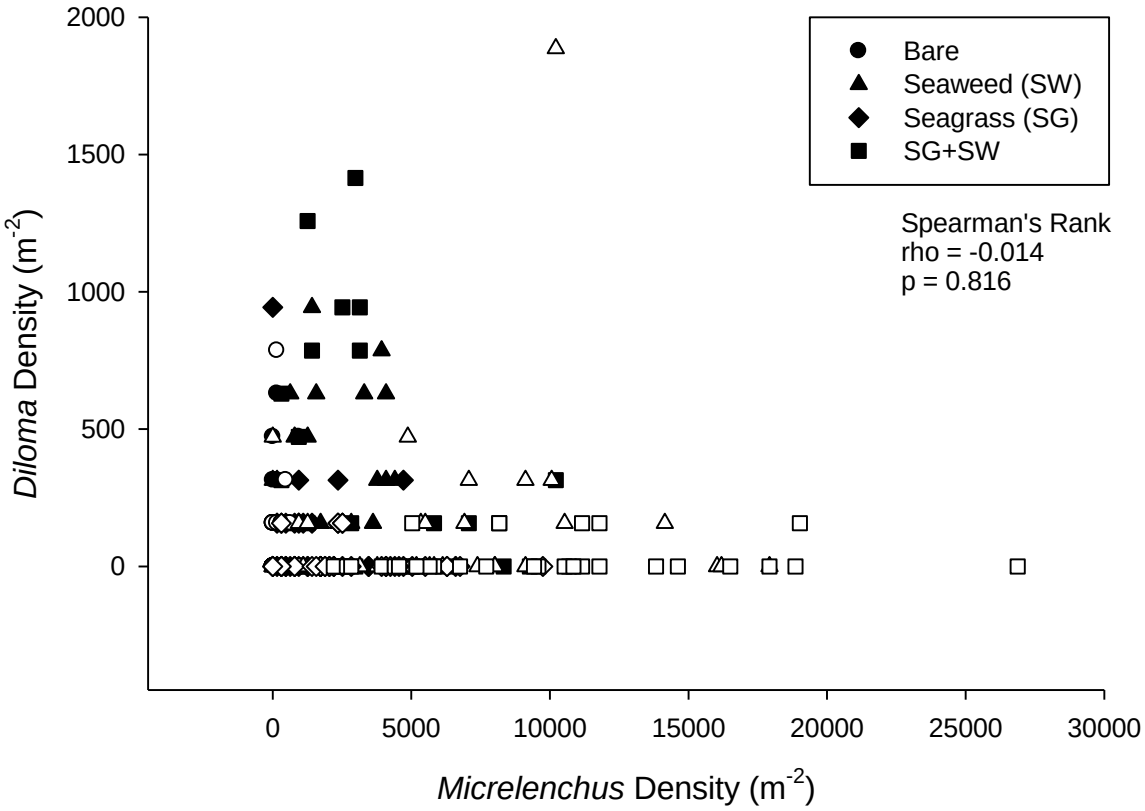


Figure 6.5 Mean densities (+SE) of *Diloma nigerrimum* and *Micrelenchus huttonii* in the Avon-Heathcote Estuary over (A) two seasons (summer *n* = 126, winter *n* = 127, each bar), (B) two sites (Plover *n* = 125, Tern *n* = 128, each bar), (C) two elevations (intertidal *n* = 128, subtidal *n* = 125, each bar), and (D) four habitats (bare *n* = 64, *Ulva n* = 61, seagrass *n* = 64, seagrass+*Ulva n* = 64, each bar). Samples were taken with benthic cylindrical cores, 9 cm diameter × 10 cm depth). SG = Seagrass bed. Note the different scales and breaks in the axes of the plots.

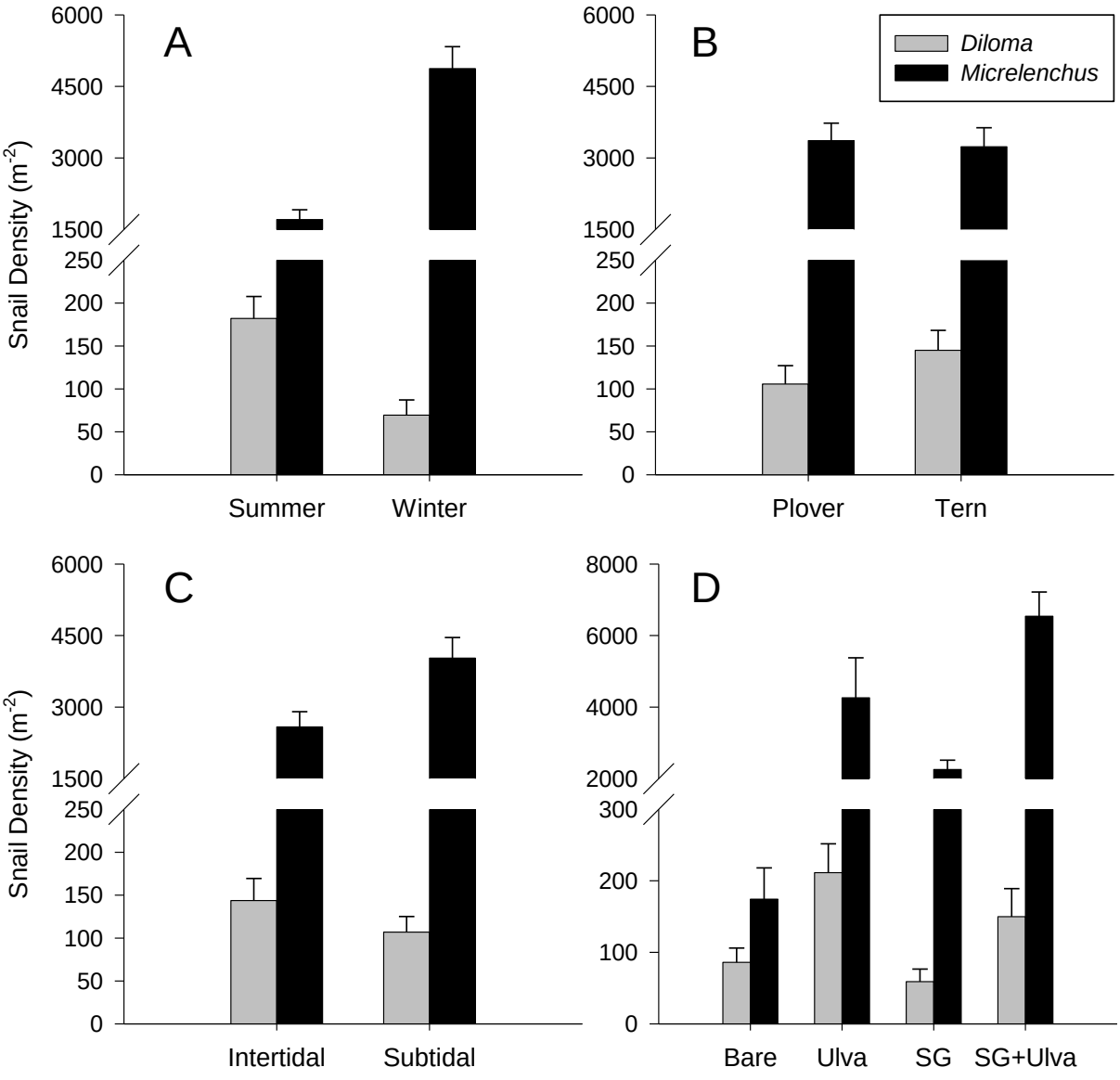


Figure 6.6 Mean grazing rates (+SE) of the estuarine trochid snails *Diloma nigerrimum* and *Micrelenchus huttonii* in lab and field experiments over 10 days. (A) a no-choice lab experiment (n = 6) with no-snail control and 4 snail treatments of 2 or 10 snails of both taxa and one food to eat: the seagrass *Zostera*, the green seaweed *Ulva*, or the red seaweed *Gracilaria*. (B) a snail-choice lab experiment (n = 6) only using the 10 snail treatments of both snails, with the addition of sediment (S), and a treatment including both *Ulva* and *Gracilaria* (U+G). The seaweed being examined is in parentheses after the treatment; i.e. U+G (G) is examining grazing rates of *Gracilaria* in the *Ulva+Gracilaria* treatment. (C) a food choice field experiment (n = 5) using only 10 *Micrelenchus*. Negative values equate to grazing, positive values equate to seaweed biomass growth.

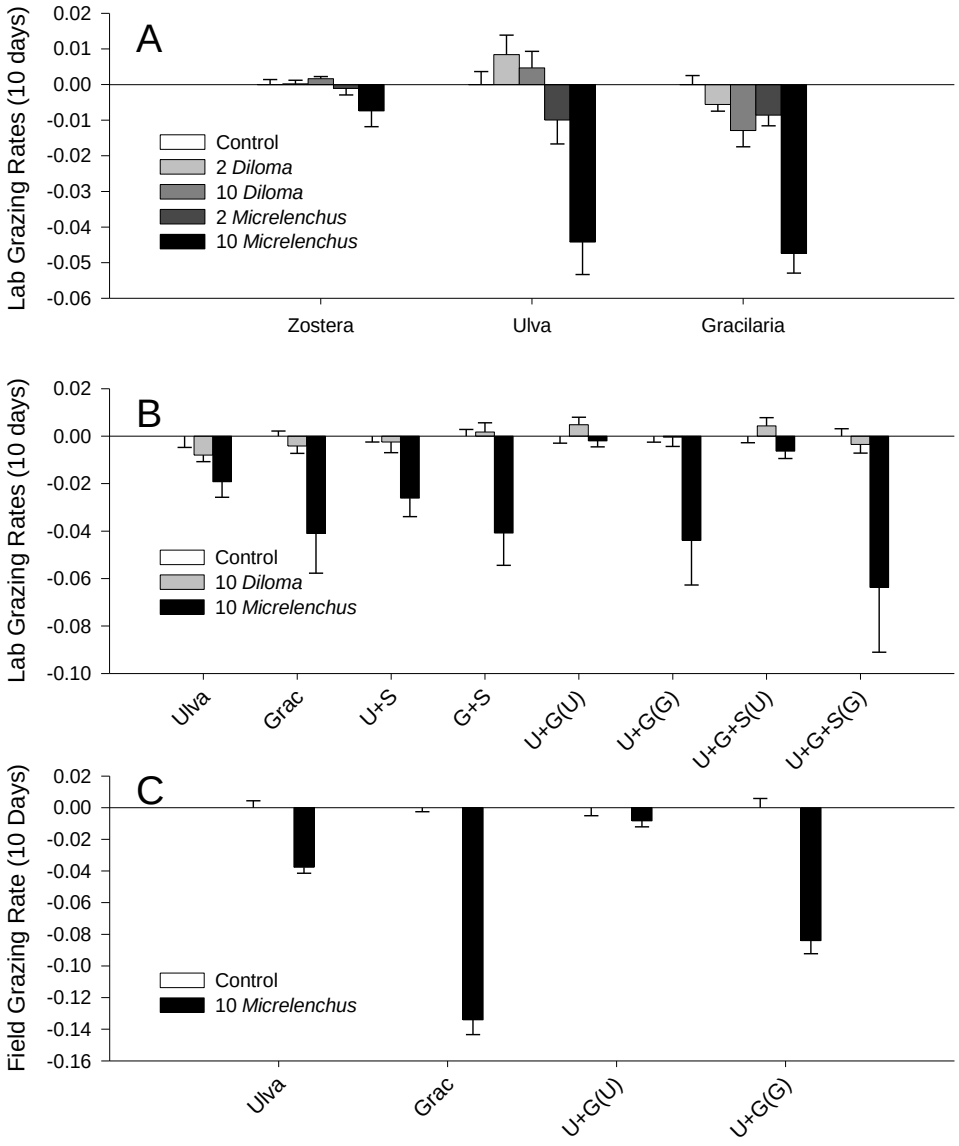
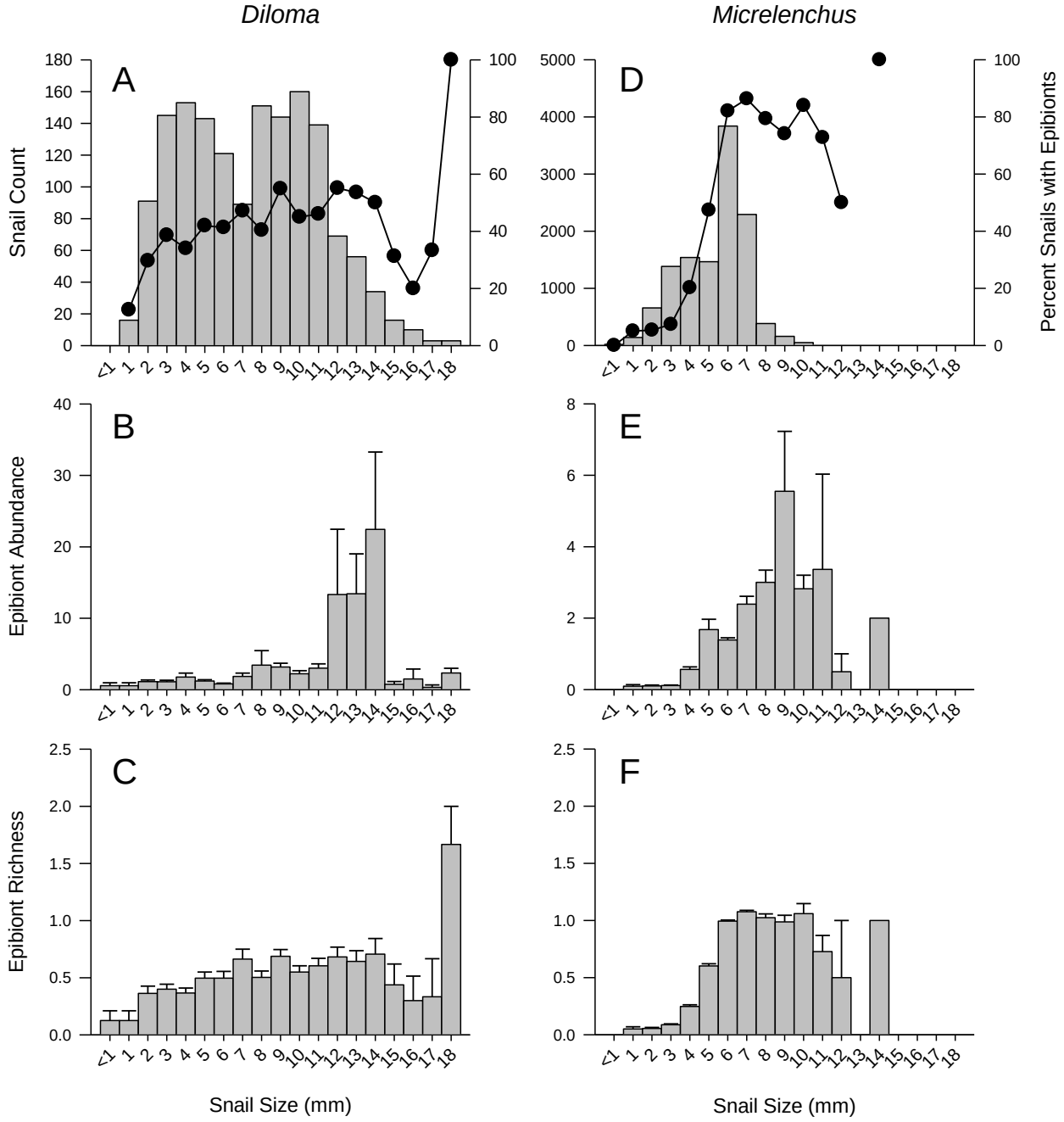


Figure 6.7 Size distributions (mm) and epibionts on the trochid snail *Diloma nigerrimum* and *Micrelenchus huttonii* in the Avon-Heathcote Estuary. (A) Size distribution of *Diloma* (bars, in mm, *n*=1543) and percent of epiphytized snails in each size class (points and line). (B) Mean ± SE number of epibionts found in each shell size category of *Diloma*. (C) Mean (+SE) richness of epibionts from each size category of *Diloma* shell sizes. (D) Size distribution of *Micrelenchus* (bars, in mm, *n*=11939) and percent of epiphytized snails in each size class (points and line). (E) Mean (+SE) number of epibionts found in each *Micrelenchus* shell size category. (F) Mean (+SE) richness of epibionts from each *Micrelenchus* size category. All snail shell sizes are lengths from bottom of aperture to top of spire.



References

Aho, J. 1978. Freshwater snail populations and the equilibrium theory of island biogeography. I. A case study in southern Finland. Annales Zoologici Fennici **15**:146-154.

Altieri, A. H., Silliman, B. R., and Bertness, M. D. 2007. Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. The American Naturalist **169**:195-206.

Altieri, A. H., Trussell, G. C., Ewanchuk, P. J., Bernatchez, G., and Bracken, M. E. S. 2009. Consumers control diversity and functioning of a natural marine ecosystem. PLoS One **4**:e5291.

Altieri, A. H., and Witman, J. D. 2014. Modular mobile foundation species as reservoirs of biodiversity. Ecosphere **5**:1-11.

Andersen, K. H., and Beyer, J. E. 2006. Asymptotic size determines species abundance in the marine size spectrum. The American Naturalist **168**:54-61.

Angelini, C., Altieri, A. H., Silliman, B. R., and Bertness, M. D. 2011. Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. BioScience **61**:782-789.

Araújo, C. V. M., Moreira-Santos, M., Patrício, J., Martins, I., Moreno-Garrido, I., Blasco, J., Marques, J. C., and Ribeiro, R. 2015. Feeding niche preference of the mudsnail *Peringia ulvae*. Marine and Freshwater Research **66**:573-581.

Battley, P. F., Melville, D. S., Schuckard, R., and Ballance, P. F. 2011. *Zostera muelleri* as a structuring agent of benthic communities in a large intertidal sandflat in New Zealand. Journal of Sea Research **65**:19-27.

Beal, B. 1994. Effects of seagrass (*Zostera marina*) cover on growth and survival of softshell clams (*Mya arenaria*). Journal of Shellfish Research **13**:311-312.

Bertness, M. D., Yund, P. O., and Brown, A. F. 1983. Snail grazing and the abundance of algal crusts on a sheltered New England rocky beach. Journal of Experimental Marine Biology and Ecology **71**:147-164.

Bonneau, E. R. 1978. Asexual reproductive capabilities in *Ulva lactuca* L. (Chlorophyceae). Botanica Marina **21**:117-121.

Boström, C., Jackson, E. L., and Simenstad, C. A. 2006. Seagrass landscapes and their effects on associated fauna: a review. Estuarine, Coastal and Shelf Science **68**:383-403.

Brönmark, C. 1985. Interactions between macrophytes, epiphytes and herbivores: an experimental approach. Oikos **45**:26-30.

Brönmark, C. 1989. Interactions between epiphytes, macrophytes and freshwater snails: a review. Journal of Molluscan Studies **55**:299-311.

Buschbaum, C., and Reise, K. 1999. Effects of barnacle epibionts on the periwinkle *Littorina littorea* (L.). Helgoland Marine Research **53**:56-61.

Cardoso, P., Pardal, M., Raffaelli, D., Baeta, A., and Marques, J. 2004. Macroinvertebrate response to different species of macroalgal mats and the role of disturbance history. Journal of Experimental Marine Biology and Ecology **308**:207-220.

Chan, D. H., and Chan, B. K. 2005. Effect of epibiosis on the fitness of the sandy shore snail *Batillaria zonalis* in Hong Kong. Marine Biology **146**:695-705.

Chen, Y. S., and Richardson, A. M. M. 1987. Factors affecting the size structure of two populations of the intertidal periwinkle, *Nodilittorina unifasciata* (Gray, 1839), in the Derwent River, Tasmania. Journal of Molluscan Studies **53**:69-78.

Choat, J. H., and Schiel, D. R. 1982. Patterns of distribution and abundance of large brown algae and invertebrate herbivores in subtidal regions of northern New Zealand. Journal of Experimental Marine Biology and Ecology **60**:129-162.

Coen, L. D. 1988. Herbivory by crabs and the control of algal epibionts on Caribbean host corals. Oecologia **75**:198-203.

Cranford, P. J. 1988. Behaviour and ecological importance of a mud snail (*Ilyanassa obsoleta*) population in a temperate macrotidal estuary. Canadian Journal of Zoology **66**:459-466.

Creese, R. G. 1988. Ecology of molluscan grazers and their interactions with marine algae in north-eastern New Zealand: a review. New Zealand Journal of Marine and Freshwater Research **22**:427-444.

Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. Pages 81-96 *in* Proceedings of the Colloquium on Conservation Problems in Antarctica. Allen Press Lawrence, Kansas, USA.

Dick, M. H., Donaldson, W. E., and Vining, I. W. 1998. Epibionts of the tanner crab *Chionoecetes bairdi* in the region of Kodiak Island, Alaska. Journal of Crustacean Biology **18**:519-527.

Edwards, D. C. 2015. Zonation by size as an adaptation for intertidal life in *Olivella biplicata*. American Zoologist **9**:399-417.

Ellison, A. M., Bank, M. S., Clinton, B. D., Colburn, E. A., Elliott, K., Ford, C. R., Foster, D. R., Kloeppel, B. D., Knoepp, J. D., and Lovett, G. M. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment **3**:479-486.

Fernández, L., Parapar, J., González-Gurriarán, E., and Muíño, R. 1998. Epibiosis and ornamental cover patterns of the spider crab *Maja squinado* on the Galician coast, northwestern Spain: influence of behavioral and ecological characteristics of the host. Journal of Crustacean Biology **18**:728-737.

Fink, P., von Elert, E., and Jüttner, F. 2006. Volatile foraging kairomones in the littoral zone: attraction of an herbivorous freshwater gastropod to algal odors. Journal of Chemical Ecology **32**:1867-1881.

Francis, M. P., Morrison, M. A., Leathwick, J., and Walsh, C. 2011. Predicting patterns of richness, occurrence and abundance of small fish in New Zealand estuaries. Marine and Freshwater Research **62**:1327-1341.

Fredriksen, S., Christie, H., and Boström, C. 2004. Deterioration of eelgrass (*Zostera marina* L.) through destructive grazing by the gastropod *Rissoa membranacea* (J. Adams). Sarsia **89**:218-222.

Gacia, E., Costalago, D., Prado, P., Piorno, D., and Tomas, F. 2009. Mesograzers in *Posidonia oceanica* meadows: an update of data on gastropod-epiphyte-seagrass interactions. Page 439 Botanica Marina.

Geertz-Hansen, O., Sand-Jensen, K., Hansen, D. F., and Christiansen, A. 1993. Growth and grazing control of abundance of the marine macroalga, *Ulva lactuca* L. In a eutrophic Danish estuary. Aquatic Botany **46**:101-109.

Giannotti, A. L., and McGlathery, K. J. 2001. Consumption of *Ulva lactuca* (Chlorophyta) by the omnivorous mud snail *Ilyanassa obsoleta* (Say). Journal of Phycology **37**:209-215.

Granado, I., and Caballero, P. 1991. Feeding preferences by *Littorina striata* King and Broderip on different algal species. SCI. MAR. **55**:577-581.

Gribben, P. E., Kimbro, D. L., Vergés, A., Gouhier, T. C., Burrell, S., Garthwin, R. G., Cagigas, M. L., Tordoff, Y., and Poore, A. G. B. 2017. Positive and negative interactions control a facilitation cascade. Ecosphere **8**:e02065.

Gribben, P. E., and Wright, J. T. 2006. Invasive seaweed enhances recruitment of a native bivalve: Roles of refuge from predation and the habitat choice of recruits. Marine Ecology Progress Series **318**:177-185.

Grove, S. L., and Probert, P. K. 1999. Sediment macrobenthos of upper Otago Harbour, New Zealand. New Zealand Journal of Marine and Freshwater Research **33**:469-480.

Guidone, M., Newton, C., and Thornber, C. S. 2014. Utilization of the invasive alga *Gracilaria vermiculophylla* (Ohmi) Papenfuss by the native mud snail *Ilyanassa obsoleta* (Say). Journal of Experimental Marine Biology and Ecology **452**:119-124.

Guidone, M., Thornber, C. S., and Field, E. 2010. Snail grazing facilitates growth of a bloom-forming alga. Marine Ecology Progress Series **420**:83-89.

Guidone, M., Thornber, C. S., and Van Alstyne, K. L. 2015. Herbivore impacts on two morphologically similar bloom-forming *Ulva* species in a eutrophic bay. Hydrobiologia **753**:175-188.
Guidone, M., Thornber, C. S., Vincent, E., and Sipes, S. 2012. Snail grazing facilitates growth of two morphologically similar bloom-forming *Ulva* species through different mechanisms. Journal of Ecology **100**:1105-1112.
Gutt, J., and Schickan, T. 1998. Epibiotic relationships in the Antarctic benthos. Antarctic Science **10**:398-405.
Haines, E. B., and Montague, C. L. 1979. Food sources of estuarine invertebrates analyzed using 13C/12C ratios. Ecology **60**:48-56.
Hauxwell, J., McClelland, J., Behr, P. J., and Valiela, I. 1998. Relative importance of grazing and nutrient controls of macroalgal biomass in three temperate shallow estuaries. Estuaries **21**:347-360.
Henriques, P. R. 1980. Faunal community structure of eight soft shore, intertidal habitats in the Manukau Harbour. New Zealand Journal of Ecology **3**:97-103.
Hily, C., Connan, S., Raffin, C., and Wyllie-Echeverria, S. 2004. In vitro experimental assessment of the grazing pressure of two gastropods on *Zostera marina* L. ephiphytic algae. Aquatic Botany **78**:183-195.
Holland, A. F., Shaughnessy, A. T., and Hiegel, M. H. 1987. Long-term variation in mesohaline Chesapeake Bay macrobenthos: spatial and temporal patterns. Estuaries **10**:227-245.
Hollever, J., and Bolton-Ritchie, L. 2016. Broad scale mapping of the estuary of the Heathcote and Avon rivers/Ihutai. Environment Canterbury.
Holzer, K. K., Rueda, J. L., and McGlathery, K. J. 2011. Differences in the feeding ecology of two seagrass-associated snails. Estuaries and Coasts **34**:1140-1149.
Iwasaki, K. 2000. Life cycle and habitat shift of the trochid snail *Diloma suavis* (Philippi) within intertidal mussel zones. Journal of Molluscan Studies **66**:9-20.
Jigyasu, H. V., and Singh, V. K. 2009. Effect of environmental factors on the fecundity, hatchability and survival of snail *Lymnaea* (Radix) *acuminata* (Lamarck): vector of fascioliasis. Journal of Water and Health **8**:109-115.
Johnson, C. R., and Mann, K. H. 1986. The importance of plant defence abilities to the structure of subtidal seaweed communities: the kelp *Laminaria longicruris* de la Pylaie survives grazing by the snail *Lacuna vincta* (Montagu) at high population densities. Journal of Experimental Marine Biology and Ecology **97**:231-267.
Jones, M. B., Marsden, I. D., and Holdaway, R. N. 2005. Life in the estuary: illustrated guide and ecology. Canterbury University Press.
Jones, M. B., and Simons, M. 1983. Latitudinal variation in reproductive characteristics of a mud crab, *Helice crassa* (Grapsidae). Bulletin of Marine Science **33**:656-670.
Kitting, C. L., Fry, B., and Morgan, M. D. 1984. Detection of inconspicuous epiphytic algae supporting food webs in seagrass meadows. Oecologia **62**:145-149.
Klumpp, D. W., Salita-Espinosa, J. S., and Fortes, M. D. 1992. The role of epiphytic periphyton and macroinvertebrate grazers in the trophic flux of a tropical seagrass community. Aquatic Botany **43**:327-349.
Krumhansl, K. A., and Scheibling, R. E. 2011. Spatial and temporal variation in grazing damage by the gastropod *Lacuna vincta* in Nova Scotian kelp beds. Aquatic Biology **13**:163-173.
Lavery, P. S., Lukatelich, R. J., and McComb, A. J. 1991. Changes in the biomass and species composition of macroalgae in a eutrophic estuary. Estuarine, Coastal and Shelf Science **33**:1-22.
Linse, K., Walker, L. J., and Barnes, D. K. 2008. Biodiversity of echinoids and their epibionts around the Scotia Arc, Antarctica. Antarctic Science **20**:227-244.
Logan, S. J. 1976. Ecology of *Diloma novaezelandiae* at Portobello, New Zealand. New Zealand Journal of Marine and Freshwater Research **10**:699-714.
Macara, G. R. 2016. Regional climatologies *in* NIWA Science and Technology Series, NIWA.

Marshall, B. A. 1998. The New Zealand recent species of *Cantharidus* Montfort, 1810 and *Micrelenchus* Finlay, 1926 (Mollusca: Gastropoda: Trochidae). Molluscan Research **19**:107-156.

McClatchie, S., Millar, R. B., Webster, F., Lester, P. J., Hurst, R., and Bagley, N. 1997. Demersal fish community diversity off New Zealand: is it related to depth, latitude and regional surface phytoplankton? Deep Sea Research Part I: Oceanographic Research Papers **44**:647-667.

McLenaghan, N. A., Tyler, A. C., Mahl, U. H., Howarth, R. W., and Marino, R. M. 2011. Benthic macroinvertebrate functional diversity regulates nutrient and algal dynamics in a shallow estuary. Marine Ecology Progress Series **426**:171-184.

Measures, R., Hicks, M., Shankar, U., Bind, J., Arnold, J., and Zeldis, J. 2011. Mapping earthquake induced topographical change and liquefaction in the Avon-Heathcote Estuary.

Miller, A. A., and Poulin, R. 2001. Parasitism, movement, and distribution of the snail *Diloma subrostrata* (Trochidae) in a soft-sediment intertidal zone. Canadian Journal of Zoology **79**:2029-2035.

Mitchell, C. P. 1980. Intertidal distribution of six trochids at Portobello, New Zealand. New Zealand Journal of Marine and Freshwater Research **14**:47-54.

Mouritsen, K. N. 2017. Periwinkle regulation: parasitism and epibiosis are linked. Marine Ecology Progress Series **579**:227-231.

Nejrup, L. B., and Pedersen, M. F. 2010. Growth and biomass development of the introduced red alga *Gracilaria vermiculophylla* is unaffected by nutrient limitation and grazing. Aquatic Biology **10**:249-259.

Nelson, T. A., Nelson, A. V., and Tjoelker, M. 2003. Seasonal and spatial patterns of "green tides" (ulvoid algal blooms) and related water quality parameters in the coastal waters of Washington State, USA. Page 263 Botanica Marina.

Nelson, W. A., Neill, K. F., and D'Archino, R. 2015. When seaweeds go bad: an overview of outbreaks of nuisance quantities of marine macroalgae in New Zealand. New Zealand Journal of Marine and Freshwater Research **49**:472-491.

NIWA. 2016. New zealand annual climate summary: 2016 *in* NIWA Research.

Norkko, A. 1998. The impact of loose-lying algal mats and predation by the brown shrimp *Crangon crangon* (L.) on infaunal prey dispersal and survival. Journal of Experimental Marine Biology and Ecology **221**:99-116.

Norkko, J., Bonsdorff, E., and Norkko, A. 2000. Drifting algal mats as an alternative habitat for benthic invertebrates: species specific responses to a transient resource. Journal of Experimental Marine Biology and Ecology **248**:79-104.

Orth, R. J., Heck, K. L., and van Montfrans, J. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries **7**:339-350.

Orth, R. J., and Van Montfrans, J. 1984. Epiphyte-seagrass relationships with an emphasis on the role of micrograzing: a review. Aquatic Botany **18**:43-69.

Palpandi, C. 2011. Hydrobiological parameters, population density and distribution pattern in the gastropod *Nerita* (*dostia*) *crepidularia* Lamarck, 1822, from mangroves of Vellar Estuary, southeast India. International Journal of Biodiversity and Conservation **3**:121-130.

Platell, M. E., and Potter, I. C. 1996. Influence of water depth, season, habitat and estuary location on the macrobenthic fauna of a seasonally closed estuary. Journal of the Marine Biological Association of the United Kingdom **76**:1-21.

Powell, A. W. B. 1979. New Zealand Mollusca: marine, land, and freshwater shells. Collins, Wellington.

Pyron, M., and Covich, A. P. 2003. Migration patterns, densities, and growth of *Neritina punctulata* snails in Rio Espiritu Santo and Rio Mameyes, northeastern Puerto Rrico. Caribbean Journal of Science, Vol. 39, No. 3, 338-347.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Raffaelli, D. G., Raven, J. A., and Poole, L. J. 1998. Ecological impact of green macroalgal blooms. Oceanography and Marine Biology: an Annual Review **36**:97-125.
Rainer, S. 1981. Temporal patterns in the structure of macrobenthic communities of an Australian estuary. Estuarine, Coastal and Shelf Science **13**:597-620.
Ramus, A. P., Silliman, B. R., Thomsen, M. S., and Long, Z. T. 2017. An invasive foundation species enhances multifunctionality in a coastal ecosystem. Proceedings of the National Academy of Sciences **114**:8580-8585.
Ren, J. S., Barr, N. G., Scheuer, K., Schiel, D. R., and Zeldis, J. 2014. A dynamic growth model of macroalgae: application in an estuary recovering from treated wastewater and earthquake-driven eutrophication. Estuarine, Coastal and Shelf Science **148**:59-69.
Sazima, C., Grossman, A., and Sazima, I. 2010. Turtle cleaners: Reef fishes foraging on epibionts of sea turtles in the tropical southwestern Aatlantic, with a summary of this association type. Neotropical Ichthyology **8**:187-192.
Schmitt, R. J., Osenberg, C. W., and Bercovitch, M. G. 1983. Mechanisms and consequences of shell fouling in the kelp snail, *Norrisia norrisi* (Sowerby) (Trochidae): Indirect effects of octopus drilling. Journal of Experimental Marine Biology and Ecology **69**:267-281.
Silliman, B. R., van de Koppel, J., Bertness, M. D., Stanton, L. E., and Mendelssohn, I. A. 2005. Drought, snails, and large-scale die-off of southern U.S. Salt marshes. Science **310**:1803-1806.
Simberloff, D. 1976. Experimental zoogeography of islands: effects of island size. Ecology **57**:629-648.
Smyth, D., and Roberts, D. 2010. The european oyster (*Ostrea edulis*) and its epibiotic succession. Hydrobiologia **655**:25-36.
Taylor, R. B. 1997. Seasonal variation in assemblages of mobile epifauna inhabiting three subtidal brown seaweeds in northeastern New Zealand. Hydrobiologia **361**:25-35.
Thieltges, D. W., and Buschbaum, C. 2007. Vicious circle in the intertidal: facilitation between barnacle epibionts, a shell boring polychaete and trematode parasites in the periwinkle *Littorina littorea*. Journal of Experimental Marine Biology and Ecology **340**:90-95.
Thivakaran, G. A., and Kasinathan, R. 1990. Salinity, temperature and desiccation tolerance of intertidal gastropods *Littorina quadricentus* and *Nodilittorina pyramidalis*.
Thomsen, M., Stæhr, P., Nejrup, L., and Schiel, D. 2013. Effects of the invasive macroalgae *Gracilaria vermiculophylla* on two co-occurring foundation species and associated invertebrates. Aquatic Invasions **8**:133-145.
Thomsen, M. S. 2010. Experimental evidence for positive effects of invasive seaweed on native invertebrates via habitat-formation in a seagrass bed. Aquatic Invasions **5**:341-346.
Thomsen, M. S., de Bettignies, T., Wernberg, T., Holmer, M., and Debeuf, B. 2012. Harmful algae are not harmful to everyone. Harmful Algae **16**:74-80.
Thomsen, M. S., Hildebrand, T., South, P. M., Foster, T., Siciliano, A., Oldach, E., and Schiel, D. R. 2016. A sixth-level habitat cascade increases biodiversity in an intertidal estuary. Ecology and evolution **6**:8291-8303.
Thomsen, M. S., McGlathery, K., Schwarzschild, A., and Silliman, B. 2009. Distribution and ecological role of the non-native macroalga *gracilaria vermiculophylla* in virginia salt marshes. Biological Invasions **11**:2303-2316.
Thomsen, M. S., and McGlathery, K. J. 2007. Stress tolerance of the invasive macroalgae codium fragile and gracilaria vermiculophylla in a soft-bottom turbid lagoon. Biological Invasions **9**:499-513.
Thomsen, M. S., and Wernberg, T. 2015. The devil in the detail: Harmful seaweeds are not harmful to everyone. Global Change Biology **21**:1381-1382.

Thomsen, M. S., Wernberg, T., Tuya, F., and Silliman, B. R. 2010. Ecological performance and possible origin of a ubiquitous but under-studied gastropod. Estuarine, Coastal and Shelf Science **87**:501-509.

Thrush, S. F., Hewitt, J. E., Hickey, C. W., and Kelly, S. 2008. Multiple stressor effects identified from species abundance distributions: interactions between urban contaminants and species habitat relationships. Journal of Experimental Marine Biology and Ecology **366**:160-168.

Thyrring, J., Thomsen, M. S., Brunbjerg, A. K., and Wernberg, T. 2015. Diversity and abundance of epibiota on invasive and native estuarine gastropods depend on substratum and salinity. Marine and Freshwater Research **66**:1191-1200.

Thyrring, J., Thomsen, M. S., and Wernberg, T. 2013. Large-scale facilitation of a sessile community by an invasive habitat-forming snail. Helgoland Marine Research **67**:789-794.

Unabia, C. R. C. 2011. The snail *Smaragdia bryanae* (Neritopsina, Neritidae) is a specialist herbivore of the seagrass *Halophila hawaiiana* (Alismatidae, Hydrocharitaceae). Invertebrate Biology **130**:100-114.

Vasconcelos, P., Cúrdia, J., Castro, M., and Gaspar, M. B. 2007. The shell of *Hexaplex* (*Trunculariopsis*) *trunculus* (Gastropoda: Muricidae) as a mobile hard substratum for epibiotic polychaetes (Annelida: Polychaeta) in the Ria Formosa (Algarve coast—southern Portugal). Hydrobiologia **575**:161-172.

Vaughn, C. C., and Fisher, F. M. 1992. Dispersion of the salt-marsh periwinkle *Littoraria irrorata*: effects of water level, size, and season. Estuaries **15**:246.

Villegas, M. J., Laudien, J., Sielfeld, W., and Arntz, W. E. 2008. *Macrocystis integrifolia* and *Lessonia trabeculata* (Laminariales; Phaeophyceae) kelp habitat structures and associated macrobenthic community off northern Chile. Helgoland Marine Research **62**:33-43.

Voight, J. R., and Walker, S. E. 1995. Geographic variation of shell bionts in the deep-sea snail *Gaza*. Deep Sea Research Part I: Oceanographic Research Papers **42**:1261-1271.

Wahl, M. 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. Marine Ecology Progress Series **58**:175-189.

Wahl, M., and Sönnichsen, H. 1992. Marine epibiosis. IV. The periwinkle *Littorina littorea* lacks typical antifouling defences - why are some populations so little fouled? Marine Ecology Progress Series **88**:225-235.

Wernberg, T., Tuya, F., Thomsen, M. S., and Kendrick, G. 2010. Turban snails as habitat for foliose algae: contrasting geographical patterns in species richness. Marine and Freshwater Research **61**:1237-1242.

Wilson, K. A., Able, K. W., and Heck Jr., K. L. 1990. Predation rates on juvenile blue crabs in estuarine nursery habitats: evidence for the importance of macroalgae (*Ulva lactuca*). Marine Ecology Progress Series **58**:243-251.

Wright, J. T., Byers, J. E., DeVore, J. L., and Sotka, E. E. 2014. Engineering or food? Mechanisms of facilitation by a habitat-forming invasive seaweed. Ecology **95**:2699-2706.

Yakovis, E. L., Artemieva, A. V., Shunatova, N. N., and Varfolomeeva, M. A. 2008. Multiple foundation species shape benthic habitat islands. Oecologia **155**:785-795.

Zacherl, D., Gaines, S. D., and Lonhart, S. I. 2003. The limits to biogeographical distributions: insights from the northward range extension of the marine snail, *Kelletia kelletii* (Forbes, 1852). Journal of Biogeography **30**:913-924.

Zeldis, J., Skilton, J., South, P., and Schiel, D. 2011. Effects of the Canterbury earthquakes on Avon-Heathcote Estuary/Ihutai ecology. NIWA Client Report No. CHC2011e **101**.

Zhang, J., Kim, J. K., Yarish, C., and He, P. 2016. The expansion of *Ulva prolifera* O.F. Müller macroalgal blooms in the Yellow Sea, PR China, through asexual reproduction. Marine Pollution Bulletin **104**:101-106.

CHAPTER 7 GENERAL DISCUSSION

In this thesis, I quantified distribution patterns and interactions between well-known estuarine foundation species (seagrass, seaweeds, and bivalves; Chapter 2-6), studied the ecology of mobile snails and dead bivalve shells, that often are overlooked as foundation species (Chapter 4, 5, 6), and quantified how estuarine benthic communities depend on these types of organisms (Chapter 4, 6). I also investigated trophic interactions between mobile foundation species and seaweed, and how estuarine foundation species affected surrounding communities through habitat-formation across spatial (latitudinal regions, estuaries, local sites, and elevation levels) and temporal (seasons, years) scales. I documented that seagrass, seaweeds, bivalves, dead bivalve shells and snails were present, and often co-occurred and interacted, across all these spatio-temporal scales. I also found that poorly researched foundation species, such as dead shells, bryozoans, and trochid snails, provide many habitat-interactions in estuaries in New Zealand.

Distributions of foundation species

Latitudinal patterns

Across latitudes of New Zealand, there were five, common, functional types of estuarine foundation species: seagrass, seaweeds, living bivalves, dead shells (mainly *Austrovenus stutchburyi*), and mobile shell-forming snails. Importantly, these foundation species commonly co-occurred within samples. For example, seagrass and seaweeds co-occurred in ca. 25% of all samples collected from 15 estuaries (Chapter 3, Figure 7.1). Abundances of both seaweed and seagrass varied between latitudinal regions, but with no clear unidirectional patterns (seagrass; central > southern > northern and seaweed; southern > northern > central). Dead bivalve shells were also ubiquitous in the estuaries (Chapter 3, Chapter 5), co-occurring with seagrasses or seaweeds in ca. 20% of all collected samples. Abundances of surface-deposited dead shells also varied with latitude (northern > southern > central, Chapter 5). Finally, mobile shell-formers were common in most, but not all surveyed estuaries (42% of all collected cores contained snails, Chapter 6). Two mobile foundation species studied in more details (the trochid snails *Diloma nigerrimum* and *Micrelenchus huttonii*) varied in density across latitudes, where *Diloma* followed a latitudinal gradient (northern > central > southern), while *Micrelenchus* was by far most abundant at central latitudes (central > northern > southern, Chapter 6). Overall, abundances of faunal foundation species (dead

shells and *Diloma*) were highest in the northern warmer region, seagrass and *Micrelenchus* in the central region, and seaweed in the southern region. Climatic variability across the 6° difference in latitude may, in part explain these patterns. For example, in 2016, the northern region received ca. 800 hours more sunlight and had 3° C higher annual mean temperature, compared to the southern region (Macara 2016, NIWA 2016). My results are similar to a pattern seen for faunal densities around New Zealand, as observed for *Austrovenus* (Studer et al. 2013), estuarine crabs (Jones and Simons 1983), and fish (Cole 2001, Francis et al. 2011) and faunal biodiversity worldwide with higher diversity in lower latitudinal regions (Fischer 1960, Stevens 1989, Rohde 1992, Hillebrand 2004). These results also support previous work that seaweeds can follow an inverse latitudinal gradient, with high densities and richness in higher latitudes (Santelices 1980, Santelices and Marquet 1998, Kerswell 2006, Keith et al. 2014, Guillemin et al. 2016).

Seasonal patterns

The distribution of the same functional types of foundation species were compared between summer and winter samples collected over a two-year period in the Avon-Heathcote Estuary. Seagrasses and seaweeds where commonly observed in the same samples, more specifically co-occurring in 62% of seasonally collected samples (Chapter 3). As expected, abundances of perennial, clonal seagrass varied relatively little between seasons (summer = winter), whereas seaweed was much more abundant in summer than winter (Chapter 3). Dead shells were also ubiquitous in the estuary and co-occurred with seagrass or seaweed in 56% of the seasonally collected samples (Chapter 3, 5) but did not vary between summer or winter months (Chapter 5). Lastly, the trochid snails *Diloma* and *Micrelenchus* co-occurred year round, and only 14% of all collected samples contained neither of these taxa (Chapter 6). Both *Diloma* and *Micrelenchus* densities were affected by season (D: summer > winter, M: winter > summer). These results support previous studies in that seagrasses provide relatively stable, year-round cover, and thereby also stable biogenic habitat and stress reduction (Chapter 1, 2, and 3) in estuaries (Virnstein and Carbonara 1985, Jackson et al. 2001, Inglis 2003, Turner and Schwarz 2006). Similarly, my results support past studies that have shown that estuarine seaweeds typically are more abundant in summer than winter – and therefore also more variable effects as a food-source and biogenic habitat (see also Chapter 1, 2, 3) (Taylor 1997, Bracken et al. 2007, Thomsen et al. 2012a, Thomsen et al. 2013, Wright et al. 2014, Dijkstra et al. 2017, Thomsen et al. 2019). Finally, dead shells and mobile foundation species were

also present year round, providing temporally stable habitat in estuaries, which concurs with results from other studies about their importance to benthic communities (Dauer et al. 1982, Kidwell 1986, Creed 2000, Gutiérrez et al. 2003, Abbott and Bergey 2007, Wernberg et al. 2010, Martins et al. 2014, Lutaenko and Levenets 2015).

Interactions among co-occurring foundation species

Seagrass and seaweeds

I found no experimental effects of seagrass on seaweed biomass or seaweed retention, whereas seaweeds had clear negative effect on both below and above ground seagrass biomass (Chapter 3, Figure 7.2). These experimental results were supported by my meta-analysis of published field and laboratory experiments; angiosperms (including seagrasses) had no significant effect on seaweeds, while seaweeds had a strong significant negative effect on angiosperms (Chapter 2, Figure 7.2). These negative effects are likely to arise through competition for light, space, and nutrients (Ceccherelli and Campo 2002, Brun et al. 2003, Taplin et al. 2005, Boese and Robbins 2008, Thomsen et al. 2012b, Thomsen et al. 2013), and, if seaweeds bloom, physical smothering and decreased oxygen levels in sediments (Valiela et al. 1997, Raffaelli et al. 1998, Nelson and Lee 2001, Nelson et al. 2015). Even though I did not find any net effects of seagrass on seaweed (Chapter 2, 3), other studies suggest that seagrasses facilitate seaweeds through physical retention of drifting unattached algae (Virnstein and Carbonara 1985, Wernberg et al. 2006, Rasmussen et al. 2013) or by providing direct attachment space for epiphytes (Orth and Van Montfrans 1984, Klumpp et al. 1992, Schanz et al. 2002, Saunders et al. 2003, Sureda et al. 2008, Lobelle et al. 2013).

Seagrass and shell-formers

Mussels added to undisturbed seagrass plots increased its below-ground biomass, but mussels added to seagrass that was already stressed (cutting seagrass leaves) had no effects (Chapter 3). This result was supported in the meta-analysis where bivalves, across all reviewed studies, had positive net effects on seagrass (Chapter 2, Figure 7.2). Seagrass, in turn, had no significant effect on bivalves (Chapter 2, Figure 7.2). I also found that seagrass had strong positive effect (through habitat-formation) on the trochid snail *Micrelenchus,* and grazing experiments showed that this snail had a small negative effect on *Zostera* (Chapter 6, Figure 7.2), By comparison *Zostera* had no effects on the morphologically similar snail species

Diloma and *Diloma* did not graze on *Zostera* (Chapter 6). Bivalves have been shown to increase porewater nutrients that can stimulate seagrass growth (Reusch and Williams 1998, Peterson and Heck Jr 2001, Booth and Heck Jr. 2009, Lohrer et al. 2016). By comparisons, seagrass can slow down currents to stimulate settlement of juvenile bivalves and snails, increase food, and provide refuge from predators (Peterson 1986, Irlandi and Peterson 1991, Judge et al. 1993, Beal 1994, Grizzle et al. 1996, Sanmartí et al. 2018). After shell-forming organisms die, their shells remain, and these hard structures may potentially interact with seagrass and other estuarine organisms (Chapter 5). Specifically, I found experimental evidence that dead shells had negative effects on aboveground seagrass biomass but no effect on belowground biomass. However, seagrass leaves did not affect retention of dead shells in experimental plots (Chapter 5, Figure 7.2). Generally, it appeared that seagrass and bivalves can facilitate each other, but when bivalves die, surface dwelling shells may reduce light levels (similar to effects of turbidity or seaweed canopies, Brun et al. 2003, Newell and Koch 2004, Ralph et al. 2007, Carroll et al. 2008) or abrade and smother seagrass leaves (Shreffler and Griffin 2000, Wagner et al. 2012).

Seaweed and shell-formers

Experimentally added live mussels had no effect on seaweed biomass (Chapter 3), a finding supported in a meta-analysis over published bivalve-seaweed experiments (Chapter 2). By contrast, the meta-analysis showed significant negative effects of seaweeds on bivalves across experimental conditions (Chapter 2, Figure 7.2). However, I found strong positive effect on mobile snails, but with much stronger positive effect on *Micrelenchus* than *Diloma* (Chapter 6). Caging experiments showed that both snails grazed on seaweed, but *Micrelenchus* had much higher grazing rates, particularly on the red seaweed *Gracilaria chilensis* (Chapter 6, Figure 7.2). Bivalves can facilitate seaweeds by increasing light penetration and water clarity through filter-feeding, allowing more photosynthesis to occur (Strayer et al. 1999, Coen et al. 2007, Zu Ermgassen et al. 2013), biodeposition of nutrients (Norkko et al. 2001, Newell 2004), and habitat provision (Sousa et al. 2009, Lutaenko and Levenets 2015, Thomsen et al. 2016, Yakovis and Artemieva 2017). The overall negative effects of seaweeds on bivalves are mostly via physical smothering, although they also can cause sediment anoxia that stress bivalves (Raffaelli et al. 1998, Thiel et al. 1998, Marsden and Bressington 2009, Marsden and Maclaren 2010). Dead bivalve shells can also facilitate seaweeds. For example, I found very high recruitment of *Ulva* onto experimentally added

shells, supporting past studies that have shown that estuarine shells provide essential limited hard substratum for sessile organisms (Chapter 5, Figure 7.2, Kidwell and Jablonski 1983, Gutiérrez et al. 2003, Thomsen 2004, Gribben and Wright 2006). Trochid snails, although small, also provided habitat for both large seaweeds, and recruits (*Diloma* > *Micrelenchus*, Chapter 6). Snails can act as 'mini-islands' of hard substrate that can increase organism biodiversity, especially epiphytic seaweeds (Schmitt et al. 1983, Thieltges and Buschbaum 2007, Wahl 2008, Wernberg et al. 2010).

Foundation species interactions with benthic communities

Invertebrates were facilitated by all foundation species studied in this thesis, including seagrasses, seaweeds, and bivalves (Chapter 3), dead shells (Chapter 5), and snails (Chapter 6), along with more cryptic organisms, like encrusting bryozoans (Chapter 4). These effects on the communities were generally affected by tidal elevation position of some foundation species (not always though), with generally higher facilitation in the lower tidal zones than in the high zones (Chapter 3, 4, 5, 6). For example, in Chapter 4, I found higher taxonomic richness of both habitat-forming organisms (foundation species) as well as habitat-users in low tidal zones in both latitudinal and seasonal surveys. Similarly, I found higher densities of the habitat-providing snail *Micrelenchus* (although not *Diloma*) in low-tidal areas (Chapter 6), and higher densities of shell-forming snails and bivalves in the Avon-Heathcote Estuary (Chapter 3). These results suggest that foundation species are important for benthic communities, but may have higher facilitative effects in certain lower-stress locations such as low-tidal zones, similar to the environmental stress model put forward by Menge and Sutherland (1987), and updated by Bruno et al. (2003), and observed in many studies worldwide (Beukema 1976, Wells 1983, Peterson 1991, Dittmann 2000, Rodrigues et al. 2006, Scrosati and Heaven 2007, Thomsen 2010, Marcías et al. 2017).

Perhaps even more importantly, when foundation species co-occurred the diversity and abundances of other invertebrates typically increased (although, sometimes not significantly so). For example, when seaweed was added experimentally to seagrass, invertebrate densities increased by 50% and 150% compared to densities in seaweed or seagrass alone (Chapter 3). Similarly, seaweeds co-occurring with dead shells also increased invertebrate densities, by 30 and 250% compared to dead shells or seaweed alone (Chapter 5). These facilitative effects

when two foundation species co-occur and affect community organization, are known as facilitation cascades (Altieri et al. 2007), and habitat cascades (Thomsen et al. 2010a), which have been reported across numerous ecosystems and habitats (Virnstein and Carbonara 1985, Powers et al. 2007, Altieri et al. 2010, Angelini et al. 2011, Watson and Herring 2012, Thomsen et al. 2013, Altieri and Witman 2014, Angelini and Silliman 2014, Thomsen and Wernberg 2014, Angelini et al. 2015, Thomsen et al. 2016, Yakovis and Artemieva 2017, Thomsen et al. 2018). Benthic estuarine organisms were also facilitated by more cryptic taxa, such as the relatively common encrusting bryozoan *Conopeum* spp. (Chapter 4). This bryozoan was often found encrusting snail shells where it increased surface roughness and facilitated recruitment in particular of different seaweed species (Chapter 4) (Thomsen et al. 2016). I also found that many other estuarine snails, in addition to *Diloma* and *Micrelenchus*) provide habitat to benthic communities, including the ubiquitous pulmonate *Amphibola crenata*, the predatory *Cominella glandiformis*, and the spired *Maoriculpus* spp. (Chapter 4). These results suggest that snails, characterized by different morphologies, sizes and habitat-preferences, provide mosaics of abundant, mobile, hard substratum in sedimentary estuaries, as shown in estuaries worldwide (Schmitt et al. 1983, Voight and Walker 1995, Wahl 1996, Creed 2000, Schories et al. 2000, Chan and Chan 2005, Thieltges and Buschbaum 2007, Thomsen et al. 2010b, Wernberg et al. 2010, Thyrring et al. 2013, Thyrring et al. 2015, Thomsen et al. 2016, Mouritsen 2017).

Conclusions

My research established that seagrasses, seaweeds, shell-forming organisms, and dead shells are foundation species that often co-occur and interact with each other in estuaries. These types of foundation species were common across estuaries in the South Island of New Zealand, in both summer and winter, although their abundances varied widely depending on environmental conditions. These organisms individually facilitated habitat-associated plants and animals, but facilitation increased when two foundation species, like seagrass and seaweed, co-occurred. I also found that overlooked dead bivalve shells, the ubiquitous bivalve *Austrovenus*, and the snails *Diloma* and *Micrelenchus* were among the most important habitat-formers in New Zealand estuaries and their impacts on estuarine communities should therefore be studied in more detail. Finally, I documented that cryptic and often overlooked species, like the bryozoan *Conopeum* spp., could also provide habitat, suggesting that more attention should be given to small species that function as intermediate

habitat-formers. I conclude that estuaries are inhabited by a myriad of co-existing foundation species that forms mosaics of biogenic habitats of varying complexity, depending on what foundation species co-occur in a microhabitat.

Figures

Figure 7.1 Proportion of collected samples with sessile (grey bars) and mobile (black bars) estuarine foundation species found in isolation or co-occurring. SG = seagrass, SW = seaweed, DS = dead shells, Dn = *Diloma nigerrimum*, Mh = *Micrelenchus huttonii*, from three latitudinal regions North (sessile N = 539, mobile N = 169 samples), Central (sessile N = 270, mobile N = 49), and South (sessile N = 525, mobile N = 160).

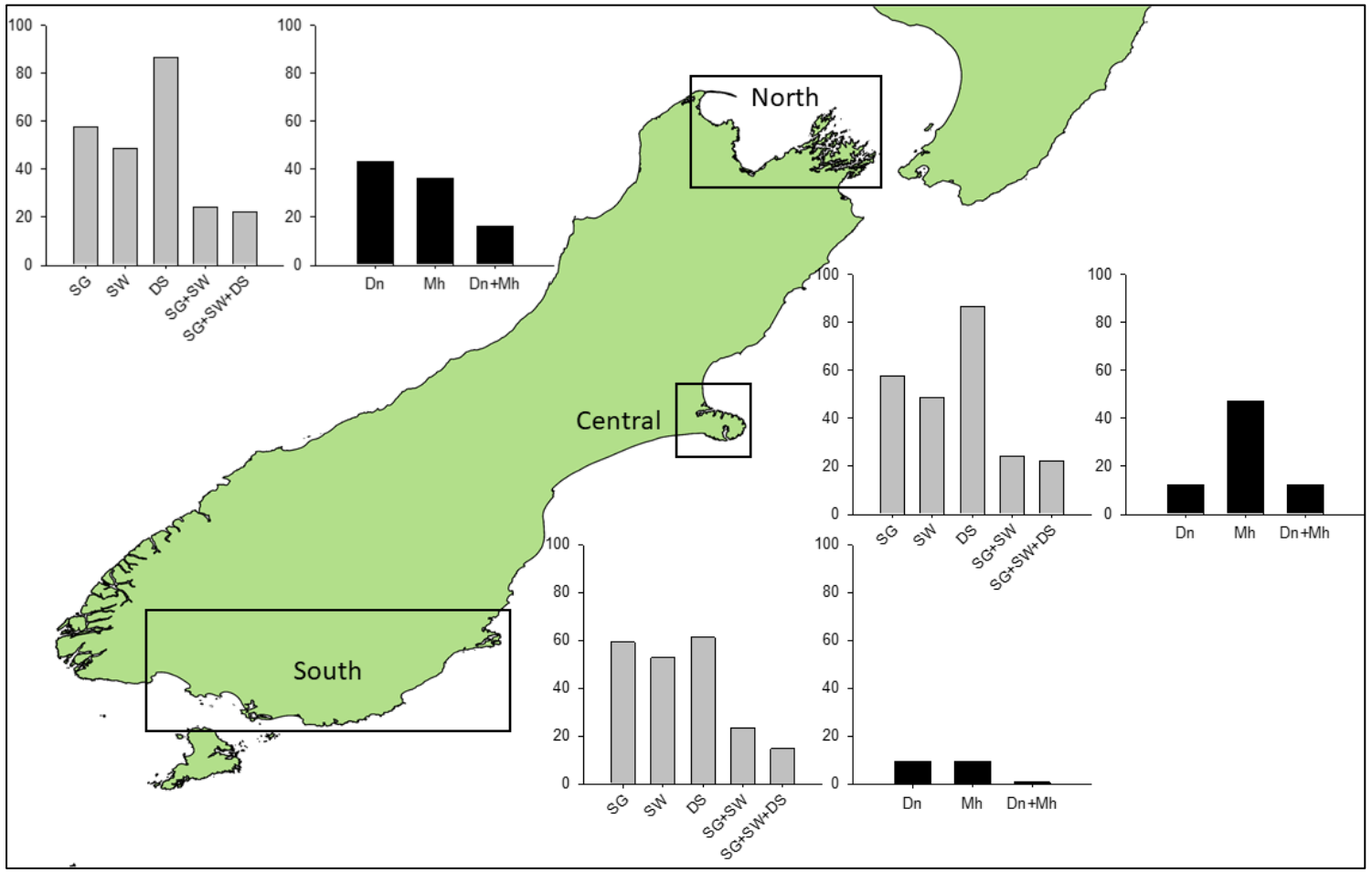
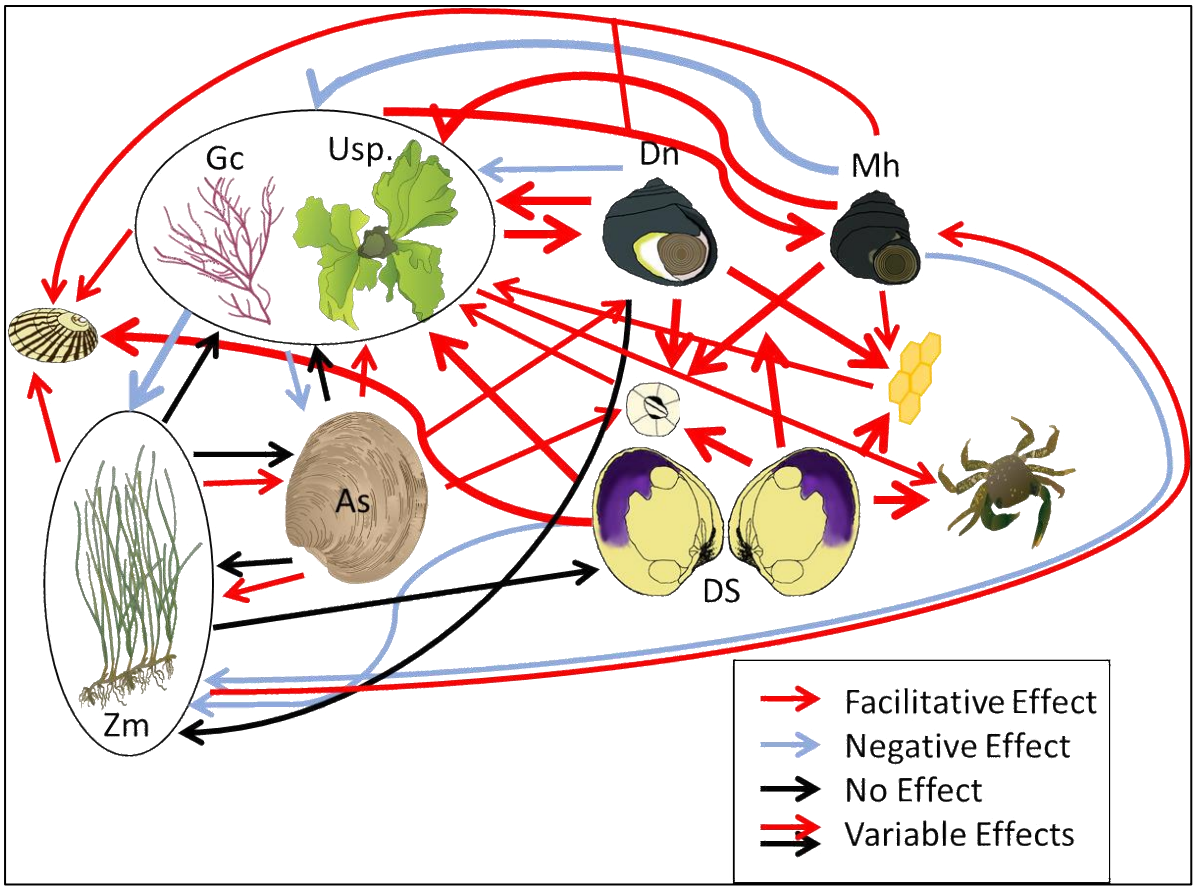


Figure 7.2 Synthesis of foundation species' effects between each other and benthic estuarine communities as described in this thesis. The direction of the arrow indicates the relationship, with the arrow point describing the recipient of the effect. Facilitative effects = red, negative effects = blue, no effect = black, while multiple arrows indicate variable effects (indicative of arrow colours) from different studies within this thesis. Facilitative effects include responses such as habitat-formation or nutrient inputs, while negative effects can include grazing or competition. Gc = *Gracilaria chilensis*, Usp. = *Ulva* spp., Zm = *Zostera muelleri*, As = *Austrovenus stutchburyi*, DS = dead shells, Dn = *Diloma nigerrimum*, and Mh = *Micrelenchus huttonii*. Larger arrows indicate importance of interactions. Graphics used are from Integration and Application Network, University of Maryland Center for Environmental Science, as well as by the author.



References

Abbott, L. L., and Bergey, E. A. 2007. Why are there few algae on snail shells? The effects of grazing, nutrients and shell chemistry on the algae on shells of *Helisoma trivolvis*. Freshwater Biology **52**:2112-2120.

Altieri, A. H., Silliman, B. R., and Bertness, M. D. 2007. Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. The American Naturalist **169**:195-206.

Altieri, A. H., van Wesenbeeck, B. K., Bertness, M. D., and Silliman, B. R. 2010. Facilitation cascade drives positive relationship between native biodiversity and invasion success. Ecology **91**:1269-1275.

Altieri, A. H., and Witman, J. D. 2014. Modular mobile foundation species as reservoirs of biodiversity. Ecosphere **5**:1-11.

Angelini, C., Altieri, A. H., Silliman, B. R., and Bertness, M. D. 2011. Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. BioScience **61**:782-789.

Angelini, C., and Silliman, B. R. 2014. Secondary foundation species as drivers of trophic and functional diversity: evidence from a tree–epiphyte system. Ecology **95**:185-196.

Angelini, C., van der Heide, T., Griffin, J. N., Morton, J. P., Derksen-Hooijberg, M., Lamers, L. P., Smolders, A. J., and Silliman, B. R. 2015. Foundation species' overlap enhances biodiversity and multifunctionality from the patch to landscape scale in southeastern United States salt marshes. Proceedings of the Royal Society B **282**:1-9.

Beal, B. F. 1994. Effects of seagrass (*Zostera marina*) cover on growth and survival of softshell clams (*Mya arenaria*). Journal of Shellfish Research **13**:311-312.

Beukema, J. J. 1976. Biomass and species richness of the macro-benthic animals living on the tidal flats of the Dutch Wadden Sea. Netherlands journal of sea research **10**:236-261.

Boese, B. L., and Robbins, B. D. 2008. Effects of erosion and macroalgae on intertidal eelgrass (*Zostera marina*) in a northeastern Pacific estuary (USA). Botanica Marina **51**:247-257.

Booth, D. M., and Heck Jr., K. L. 2009. Effects of the american oyster *Crassostrea virginica* on growth rates of the seagrass *Halodule wrightii*. Marine Ecology Progress Series **389**:117-126.

Bracken, M. E., Gonzalez-Dorantes, C. A., and Stachowicz, J. J. 2007. Whole-community mutualism: associated invertebrates facilitate a dominant habitat-forming seaweed. Ecology **88**:2211-2219.

Brun, F. G., Vergara, J. J., Navarro, G., Hernández, I., and Pérez-Lloréns, J. L. 2003. Effect of shading by *Ulva rigida* canopies on growth and carbon balance of the seagrass *Zostera noltii*. Marine Ecology Progress Series **265**:85-96.

Bruno, J. F., Stachowicz, J. J., and Bertness, M. D. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology & Evolution **18**:119-125.

Carroll, J., Gobler, C. J., and Peterson, B. J. 2008. Resource-restricted growth of eelgrass in New York estuaries: light limitation, and alleviation of nutrient stress by hard clams. Marine Ecology Progress Series **369**:51-62.

Ceccherelli, G., and Campo, D. 2002. Different effects of *Caulerpa racemosa* on two co-occurring seagrasses in the Mediterranean. Botanica Marina **45**:71-76.

Chan, D. H., and Chan, B. K. 2005. Effect of epibiosis on the fitness of the sandy shore snail *Batillaria zonalis* in Hong Kong. Marine Biology **146**:695-705.

Coen, L. D., Brumbaugh, R. D., Bushek, D., Grizzle, R., Luckenbach, M. W., Posey, M. H., Powers, S. P., and Tolley, S. 2007. Ecosystem services related to oyster restoration. Marine Ecology Progress Series **341**:303-307.

Cole, R. G. 2001. Patterns of abundance and population size structure of herbivorous fishes at the subtropical Kermadec Islands and in mainland New Zealand. New Zealand Journal of Marine and Freshwater Research **35**:445-456.

Creed, J. C. 2000. Epibiosis on cerith shells in a seagrass bed: correlation of shell occupant with epizoite distribution and abundance. Marine Biology **137**:775-782.

Dauer, D., Tourtellotte, G., and Ewing, R. 1982. Oyster shells and artificial worm tubes: the role of refuges in structuring benthic communities of the lower Chesapeake Bay. Internationale Revue der Gesamten Hydrobiologie und Hydrographie **67**:661-677.

Dijkstra, J. A., Harris, L. G., Mello, K., Litterer, A., Wells, C., and Ware, C. 2017. Invasive seaweeds transform habitat structure and increase biodiversity of associated species. Journal of Ecology **105**:1668-1678.

Dittmann, S. 2000. Zonation of benthic communities in a tropical tidal flat of north-east Australia. Journal of Sea Research **43**:33-51.

Fischer, A. G. 1960. Latitudinal variations in organic diversity. Evolution **14**:64-81.

Francis, M. P., Morrison, M. A., Leathwick, J., and Walsh, C. 2011. Predicting patterns of richness, occurrence and abundance of small fish in New Zealand estuaries. Marine and Freshwater Research **62**:1327-1341.

Gribben, P. E., and Wright, J. T. 2006. Invasive seaweed enhances recruitment of a native bivalve: roles of refuge from predation and the habitat choice of recruits. Marine Ecology Progress Series **318**:177-185.

Grizzle, R. E., Short, F. T., Newell, C. R., Hoven, H., and Kindblom, L. 1996. Hydrodynamically induced synchronous waving of seagrasses:'monami'and its possible effects on larval mussel settlement. Journal of Experimental Marine Biology and Ecology **206**:165-177.

Guillemin, M.-L., Valero, M., Tellier, F., Macaya, E. C., Destombe, C., and Faugeron, S. 2016. Phylogeography of seaweeds in the south east Pacific: complex evolutionary processes along a latitudinal gradient. Pages 251-277 *in* Z.-M. Hu and C. Fraser, editors. Seaweed Phylogeography: Adaptation and Evolution of Seaweeds under Environmental Change. Springer Netherlands, Dordrecht.

Gutiérrez, J. L., Jones, C. G., Strayer, D. L., and Iribarne, O. O. 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos **101**:79-90.

Hillebrand, H. 2004. Strength, slope and variability of marine latitudinal gradients. Marine Ecology Progress Series **273**:251-267.

Inglis, G. 2003. Seagrasses of New Zealand. Pages 134-143 *in* E. P. Green and F. T. Short, editors. World Atlas of Seagrasses: Present Status and Future Conservation. University of California Press, Berkeley, California.

Irlandi, E. A., and Peterson, C. H. 1991. Modification of animal habitat by large plants: mechanisms by which seagrasses influence clam growth. Oecologia **87**:307-318.

Jackson, E. L., Rowden, A. A., Attrill, M. J., Bossey, S. J., and Jones, M. B. 2001. The importance of seagrass beds as a habitat for fishery species. Pages 269-304 *in* R. N. Gibson, M. Barnes, and R. J. A. Atkinson, editors. Oceanography & marine biology: An annual review. Taylor & Francis Inc., New York, NY.

Jones, M. B., and Simons, M. 1983. Latitudinal variation in reproductive characteristics of a mud crab, *Helice crassa* (Grapsidae). Bulletin of Marine Science **33**:656-670.

Judge, M. L., Coen, L. D., and Heck Jr, K. L. 1993. Does *Mercenaria mercenaria* encounter elevated food levels in seagrass beds? Results from a novel technique to collect suspended food resources. Marine Ecology Progress Series **92**:141-150.

Keith, S. A., Kerswell, A. P., and Connolly, S. R. 2014. Global diversity of marine macroalgae: Environmental conditions explain less variation in the tropics. Global Ecology and Biogeography **23**:517-529.

Kerswell, A. P. 2006. Global biodiversity patterns of benthic marine algae. Ecology **87**:2479-2488.

Kidwell, S. M. 1986. Taphonomic feedback in Miocene assemblages: testing the role of dead hardparts in benthic communities. Palaios **1**:239-255.

Kidwell, S. M., and Jablonski, D. 1983. Taphonomic feedback: Ecological consequences of shell accumulation. Pages 195-248 *in* M. J. S. Tevesz and P. L. McCall, editors. Biotic Interactions in Recent and Fossil Benthic Communities. Springer US, Boston, MA.

Klumpp, D. W., Salita-Espinosa, J. S., and Fortes, M. D. 1992. The role of epiphytic periphyton and macroinvertebrate grazers in the trophic flux of a tropical seagrass community. Aquatic Botany **43**:327-349.

Lobelle, D., Kenyon, E. J., Cook, K. J., and Bull, J. C. 2013. Local competition and metapopulation processes drive long-term seagrass-epiphyte population dynamics. PLoS One **8**:e57072.

Lohrer, A. M., Townsend, M., Hailes, S. F., Rodil, I. F., Cartner, K., Pratt, D. R., and Hewitt, J. E. 2016. Influence of New Zealand cockles (*Austrovenus stutchburyi*) on primary productivity in sandflat-seagrass (*Zostera muelleri*) ecotones. Estuarine, Coastal and Shelf Science **181**:238-248.

Lutaenko, K. A., and Levenets, I. R. 2015. Observations on seaweed attachment to bivalve shells in Peter the Great Bay (East Sea) and their taphonomic implications. Korean Journal of Malacology **31**:221-232.

Macara, G. R. 2016. Regional climatologies *in* NIWA Science and Technology Series, NIWA.

Marcías, M. L., Deregibus, D., Saravia, L. A., Campana, G. L., and Quartino, M. L. 2017. Life between tides: Spatial and temporal variations of an intertidal macroalgal community at Potter Peninsula, South Shetland Islands, Antarctica. Estuarine, Coastal and Shelf Science **187**:193-203.

Marsden, I. D., and Bressington, M. J. 2009. Effects of macroalgal mats and hypoxia on burrowing depth of the New Zealand cockle (*Austrovenus stutchburyi*). Estuarine, Coastal and Shelf Science **81**:438-444.

Marsden, I. D., and Maclaren, S. R. 2010. Short-term study testing the resilience of an estuarine bivalve to macroalgal mats. Hydrobiologia **649**:217-229.

Martins, G. M., Faria, J., Furtado, M., and Neto, A. I. 2014. Shells of *Patella aspera* as 'islands' for epibionts. Journal of the Marine Biological Association of the United Kingdom **94**:1027-1032.

Menge, B. A., and Sutherland, J. P. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. The American Naturalist **130**.

Mouritsen, K. N. 2017. Periwinkle regulation: Parasitism and epibiosis are linked. Marine Ecology Progress Series **579**:227-231.

Nelson, T. A., and Lee, A. 2001. A manipulative experiment demonstrates that blooms of the macroalga *ulvaria obscura* can reduce eelgrass shoot density. Aquatic Botany **71**:149-154.

Nelson, W. A., Neill, K. F., and D'Archino, R. 2015. When seaweeds go bad: An overview of outbreaks of nuisance quantities of marine macroalgae in new zealand. New Zealand Journal of Marine and Freshwater Research **49**:472-491.

Newell, R. I. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. Journal of Shellfish Research **23**:51-62.

Newell, R. I., and Koch, E. W. 2004. Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. Estuaries **27**:793-806.

NIWA. 2016. New Zealand annual climate summary: 2016. NIWA Research.

Norkko, A., Hewitt, J. E., Thrush, S. F., and Funnell, T. 2001. Benthic-pelagic coupling and suspension-feeding bivalves: linking site-specific sediment flux and biodeposition to benthic community structure. Limnology and Oceanography **46**:2067-2072.

Orth, R. J., and Van Montfrans, J. 1984. Epiphyte-seagrass relationships with an emphasis on the role of micrograzing: a review. Aquatic Botany **18**:43-69.

Peterson, B. J., and Heck Jr, K. L. 2001. Positive interactions between suspension-feeding bivalves and seagrass-a facultative mutualism. Marine Ecology Progress Series **213**:143-155.

Peterson, C. H. 1986. Enhancement of *Mercenaria mercenaria* densities in seagrass beds: is pattern fixed during settlement season or altered by subsequent differential survival? Limnology and Oceanography **31**:200-205.

Peterson, C. H. 1991. Intertidal zonation of marine invertebrates in sand and mud. American Scientist **79**:236-249.

Powers, M. J., Peterson, C. H., Summerson, H. C., and Powers, S. P. 2007. Macroalgal growth on bivalve aquaculture netting enhances nursery habitat for mobile invertebrates and juvenile fishes. Marine Ecology Progress Series **339**:109-122.

Raffaelli, D. G., Raven, J. A., and Poole, L. J. 1998. Ecological impact of green macroalgal blooms. Oceanography and Marine Biology: an annual review **36**:97-125.

Ralph, P. J., Durako, M. J., Enríquez, S., Collier, C. J., and Doblin, M. A. 2007. Impact of light limitation on seagrasses. Journal of Experimental Marine Biology and Ecology **350**:176-193.

Rasmussen, J. R., Pedersen, M. F., Olesen, B., Nielsen, S. L., and Pedersen, T. M. 2013. Temporal and spatial dynamics of ephemeral drift-algae in eelgrass, *Zostera marina*, beds. Estuarine, Coastal and Shelf Science **119**:167-175.

Reusch, T. B., and Williams, S. L. 1998. Variable responses of native eelgrass *Zostera marina* to a non-indigenous bivalve *Musculista senhousia*. Oecologia **113**:428-441.

Rodrigues, A. M., Meireles, S., Pereira, T., Gama, A., and Quintino, V. 2006. Spatial patterns of benthic macroinvertebrates in intertidal areas of a southern European estuary: The Tagus, Portugal. Pages 99-113 *in* K. Martens, H. Queiroga, M. R. Cunha, A. Cunha, M. H. Moreira, V. Quintino, A. M. Rodrigues, J. Seroôdio, and R. M. Warwick, editors. Marine Biodiversity: Patterns and Processes, Assessment, Threats, Management and Conservation. Springer Netherlands, Dordrecht.

Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. Oikos **65**:514-527.

Sanmartí, N., Solé, L., Romero, J., and Pérez, M. 2018. Seagrass-bivalve facilitative interactions: trait-mediated effects along an environmental gradient. Marine Environmental Research **133**:99-104.

Santelices, B. 1980. Phytogeographic characterization of the temperate coast of Pacific South America. Phycologia **19**:1-12.

Santelices, B., and Marquet, P. 1998. Seaweeds, latitudinal diversity patterns, and Rapoport's rule. Diversity and Distributions **4**:71-75.

Saunders, J. E., Attrill, M. J., Shaw, S. M., and Rowden, A. A. 2003. Spatial variability in the epiphytic algal assemblages of *Zostera marina* seagrass beds. Marine Ecology Progress Series **249**:107-115.

Schanz, A., Polte, P., and Asmus, H. 2002. Cascading effects of hydrodynamics on an epiphyte–grazer system in intertidal seagrass beds of the Wadden Sea. Marine Biology **141**:287-297.

Schmitt, R. J., Osenberg, C. W., and Bercovitch, M. G. 1983. Mechanisms and consequences of shell fouling in the kelp snail, *Norrisia norrisi* (Sowerby) (Trochidae): indirect effects of octopus drilling. Journal of Experimental Marine Biology and Ecology **69**:267-281.

Schories, D., Anibal, J., Chapman, A. S., Herre, E., Isaksson, I., Lillebø¸ Ana, I., Pihl, L., Reise, K., Sprung, M., and Thiel, M. 2000. Flagging greens: hydrobiid snails as substrata for the development of green algal mats (*Enteromorpha* spp.) on tidal flats of North Atlantic coasts. Marine Ecology Progress Series **199**:127-136.

Scrosati, R., and Heaven, C. 2007. Spatial trends in community richness, diversity, and evenness across rocky intertidal environmental stress gradients in eastern Canada. Marine Ecology Progress Series **342**:1-14.

Shreffler, D. K., and Griffin, K. 2000. Ecological interactions among eelgrass, oysters, and burrowing shrimp in Tillamook Bay, Oregon: Year 2 (1999) Report. Pages 1-53 *in* T. C. P. Partnership, editor. Tillamook County Performance Partnership, Garabaldi, OR.

Sousa, R., Gutiérrez, J., and Aldridge, D. 2009. Non-indigenous invasive bivalves as ecosystem engineers. Biological Invasions **11**:2367-2385.

Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. The American Naturalist **133**:240-256.

Strayer, D. L., Caraco, N. F., Cole, J. J., Findlay, S., and Pace, M. L. 1999. Transformation of freshwater ecosystems by bivalves. BioScience **49**:19-27.

Studer, A., Widmann, M., Poulin, R., and Krkošek, M. 2013. Large scale patterns of trematode parasitism in a bivalve host: no evidence for a latitudinal gradient in infection levels. Marine Ecology Progress Series **491**:125-135.

Sureda, A., Box, A., Terrados, J., Deudero, S., and Pons, A. 2008. Antioxidant response of the seagrass *Posidonia oceanica* when epiphytized by the invasive macroalgae *Lophocladia lallemandii*. Marine Environmental Research **66**:359-363.

Taplin, K. A., Irlandi, E. A., and Raves, R. 2005. Interference between the macroalga *Caulerpa prolifera* and the seagrass *Halodule wrightii*. Aquatic Botany **83**:175-186.

Taylor, R. B. 1997. Seasonal variation in assemblages of mobile epifauna inhabiting three subtidal brown seaweeds in northeastern New Zealand. Hydrobiologia **361**:25-35.

Thiel, M., Stearns, L., and Watling, L. 1998. Effects of green algal mats on bivalves in a New England mud flat. Helgoländer Meeresuntersuchungen **52**:15-28.

Thieltges, D. W., and Buschbaum, C. 2007. Vicious circle in the intertidal: facilitation between barnacle epibionts, a shell boring polychaete and trematode parasites in the periwinkle *Littorina littorea*. Journal of Experimental Marine Biology and Ecology **340**:90-95.

Thomsen, M., Stæhr, P., Nejrup, L., and Schiel, D. 2013. Effects of the invasive macroalgae *Gracilaria vermiculophylla* on two co-occurring foundation species and associated invertebrates. Aquatic Invasions **8**:133-145.

Thomsen, M. S. 2004. Species, thallus size and substrate determine macroalgal break force and break location in a low-energy soft-bottom lagoon. Aquatic Botany **80**:153-161.

Thomsen, M. S. 2010. Experimental evidence for positive effects of invasive seaweed on native invertebrates via habitat-formation in a seagrass bed. Aquatic Invasions **5**:341-346.

Thomsen, M. S., Altieri, A. H., Angelini, C., Bishop, M. J., Gribben, P. E., Lear, G., He, Q., Schiel, D. R., Silliman, B. R., South, P. M., Watson, D. M., Wernberg, T., and Zotz, G. 2018. Secondary foundation species enhance biodiversity. Nature Ecology & Evolution **2**:634-639.

Thomsen, M. S., de Bettignies, T., Wernberg, T., Holmer, M., and Debeuf, B. 2012a. Harmful algae are not harmful to everyone. Harmful Algae **16**:74-80.

Thomsen, M. S., Hildebrand, T., South, P. M., Foster, T., Siciliano, A., Oldach, E., and Schiel, D. R. 2016. A sixth-level habitat cascade increases biodiversity in an intertidal estuary. Ecology and Evolution **6**:8291-8303.

Thomsen, M. S., Ramus, A. P., Long, Z. T., and Silliman, B. R. 2019. A seaweed increases ecosystem multifunctionality when invading bare mudflats. Biological Invasions **21**:27-36.

Thomsen, M. S., and Wernberg, T. 2014. On the generality of cascading habitat-formation. Proceedings of the Royal Society B: Biological Sciences **281**:20131994.

Thomsen, M. S., Wernberg, T., Altieri, A., Tuya, F., Gulbransen, D., McGlathery, K. J., Holmer, M., and Silliman, B. R. 2010a. Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. Integrative and Comparative Biology **50**:158-175.

Thomsen, M. S., Wernberg, T., Engelen, A. H., Tuya, F., Vanderklift, M. A., Holmer, M., McGlathery, K. J., Arenas, F., Kotta, J., and Silliman, B. R. 2012b. A meta-analysis of seaweed impacts on seagrasses: generalities and knowledge gaps. PLoS One **7**:1-8.

Thomsen, M. S., Wernberg, T., Tuya, F., and Silliman, B. R. 2010b. Ecological performance and possible origin of a ubiquitous but under-studied gastropod. Estuarine, Coastal and Shelf Science **87**:501-509.

Thyrring, J., Thomsen, M. S., Brunbjerg, A. K., and Wernberg, T. 2015. Diversity and abundance of epibiota on invasive and native estuarine gastropods depend on substratum and salinity. Marine and Freshwater Research **66**:1191-1200.

Thyrring, J., Thomsen, M. S., and Wernberg, T. 2013. Large-scale facilitation of a sessile community by an invasive habitat-forming snail. Helgoland Marine Research **67**:789-794.

Turner, S., and Schwarz, A.-M. 2006. Management and conservation of seagrass in New Zealand: an introduction. Science for Conservation 264:1-90.
Valiela, I., McClelland, J., Hauxwell, J., Behr, P. J., Hersh, D., and Foreman, K. 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnology and Oceanography **42**:1105-1118.
Virnstein, R. W., and Carbonara, P. A. 1985. Seasonal abundance and distribution of drift algae and seagrasses in the Mid-Indian River Lagoon, Florida. Aquatic Botany **23**:67-82.
Voight, J. R., and Walker, S. E. 1995. Geographic variation of shell bionts in the deep-sea snail *Gaza*. Deep Sea Research Part I: Oceanographic Research Papers **42**:1261-1271.
Wagner, E., Dumbauld, B. R., Hacker, S. D., Trimble, A. C., Wisehart, L. M., and Ruesink, J. L. 2012. Density-dependent effects of an introduced oyster, *Crassostrea gigas*, on a native intertidal seagrass, *Zostera marina*. Marine Ecology Progress Series **468**:149-160.
Wahl, M. 1996. Fouled snails in flow: potential of epibionts on *Littorina littorea* to increase drag and reduce snail growth rates. Marine Ecology Progress Series **138**:157-168.
Wahl, M. 2008. Ecological lever and interface ecology: epibiosis modulates the interactions between host and environment. Biofouling **24**:427-438.
Watson, D. M., and Herring, M. 2012. Mistletoe as a keystone resource: an experimental test. Proceedings of the Royal Society of London B: Biological Sciences **279**:3853–3860.
Wells, F. E. 1983. An analysis of marine invertebrate distributions in a mangrove swamp in northwestern Australia. Bulletin of Marine Science **33**:736-744.
Wernberg, T., Tuya, F., Thomsen, M. S., and Kendrick, G. 2010. Turban snails as habitat for foliose algae: contrasting geographical patterns in species richness. Marine and Freshwater Research **61**:1237-1242.
Wernberg, T., Vanderklift, M. A., How, J., and Lavery, P. S. 2006. Export of detached macroalgae from reefs to adjacent seagrass beds. Oecologia **147**:692-701.
Wright, J. T., Byers, J. E., DeVore, J. L., and Sotka, E. E. 2014. Engineering or food? Mechanisms of facilitation by a habitat-forming invasive seaweed. Ecology **95**:2699-2706.
Yakovis, E., and Artemieva, A. 2017. Cockles, barnacles and ascidians compose a subtidal facilitation cascade with multiple hierarchical levels of foundation species. Scientific Reports **7**:237.
Zu Ermgassen, P. S., Spalding, M. D., Grizzle, R. E., and Brumbaugh, R. D. 2013. Quantifying the loss of a marine ecosystem service: filtration by the eastern oyster in US estuaries. Estuaries and Coasts **36**:36-43.